When do traits tell more than species about a metacommunity? A synthesis across ecosystems and scales

Alienor Jeliazkov, Jonathan Chase

To cite this version:

Alienor Jeliazkov, Jonathan Chase. When do traits tell more than species about a metacommunity? A synthesis across ecosystems and scales. The American Naturalist, 2023, 10.1086/727471 . hal-04186831

HAL Id: hal-04186831
https://hal.inrae.fr/hal-04186831

Submitted on 28 Aug 2023

Title page

When do traits tell more than species about a metacommunity? A synthesis across ecosystems and scales

Authors

Alienor Jeliazkov[1] & Jonathan M. Chase[2,3]

ORCIDS

Alienor Jeliazkov: 0000-0001-5765-3721

Jonathan M. Chase: 0000-0001-5580-4303

Affiliations

[1] University of Paris-Saclay, INRAE, HYCAR, 1 rue Pierre Gilles de Gennes, 92160 Antony, France

[2] German Centre for Integrative Biodiversity Research (iDiv), Deutscher Platz 5E, 04103 Leipzig, Germany

[3] Department of Computer Science, Martin Luther University Halle-Wittenberg, 06099 Halle (Salle), Germany

Corresponding author: Alienor Jeliazkov: alienor.jeliazkov@gmail.com; alienor.jeliazkov@inrae.fr

Running head: Species traits in metacommunity ecology

Keywords: Species, traits, environment, beta diversity, functional, taxonomic

Number of words in the text (excl. References and Figure legends): 6322

Type of article: E-Article

List of the elements of the paper:

- Main MS
- 1 table
- 5 figures
- 1 Supplementary Information PDF

Abstract

Linking species traits with the variation in species assemblages across habitats has often proved useful for developing a more mechanistic understanding of species distributions in metacommunities. However, by summarizing the rich tapestry of a species in all of its nuance to a few key ecological traits can also lead to an abstraction that provides less predictability than when using taxonomy alone. As a further complication, taxonomic and functional diversities can be inequitably compared, either by integrating taxonomic-level information into the calculation of how functional aspects of communities vary, or by detecting spurious trait-environment relationships. To remedy this, we here synthesize analyses of 80 datasets on different taxa, ecosystems and spatial scales that include information on abundance or presence/absence of species across sites with variable environmental conditions, and the species' traits. By developing analyses that treat functional and taxonomic diversity equitably, we ask when functional diversity helps to explain metacommunity structure. We found that patterns of functional diversity explained metacommunity structure and response to environmental variation in only 25% of the datasets using a multi-trait approach, but up to 59% using a single-trait approach. Nevertheless, an average of only 19% (interquartile range=0-29%) of the traits showed a significant signal across environmental gradients. Species-level traits, as typically collected and analyzed through functional diversity patterns, often do not bring predictive advantages over what the taxonomic information already holds. While our assessment of a limited advantage of using traits to explain variation in species assemblages was largely true across ecosystems, traits played a more useful role in explaining variation when many traits were used, and when trait constructs were more related to species' status, life history, and mobility. We propose future research directions to make trait-based approaches and data more helpful for inference in metacommunity ecology.

Introduction

Metacommunity ecology aims to understand and predict how patterns of biodiversity and community composition are structured through space and time, and how those patterns are determined by a number of underlying processes, including biotic interactions, environmental control, dispersal, and ecological drift (Leibold and Chase 2017; Thompson et al. 2020). To this aim, the analysis of the variation of assemblage composition across space—often referred to as beta-diversity (Whittaker 1960)—is central in metacommunity ecology (e.g. Leibold and Chase 2017; Ruhí et al. 2017; Mori et al. 2018; Chase et al. 2020). This is because compositional variation through space, by keeping track of taxonomic identities across sites, can be more informative about community assembly processes than patterns of diversity within a site can (i.e., two sites can have similar diversity, but very different composition). By analyzing compositional variation, one can begin to disentangle the signatures from different structuring processes, such as the relative importance of niche vs. neutral assembly processes (Cottenie 2005; Chase and Myers 2011; Soininen 2014, 2016). Usually, these inductive analyses are achieved either with the use of null modelling approaches (e.g. Chase et al. 2011; Tucker et al. 2016), or the relative importance of environmental and spatial drivers of the community structuring (Peres-Neto et al. 2006; Tuomisto and Ruokolainen 2006, 2008; Legendre et al. 2009; Soininen 2014, 2016).

Studies that use only taxonomic information, even when using the best available methods, typically only explain a small amount of the variation in community composition (Ovaskainen et al. 2019; Guzman et al. 2022) and have limited ability for prediction (Viana et al. 2022) and inference (Gilbert and Bennett 2010; Smith and Lundholm 2010; Viana and Chase 2019). A popular solution to this limited inferential ability of taxonomic patterns is to include functional information on species traits (Lavorel and Garnier 2002; McGill et al. 2006; Shipley et al. 2012; Cadotte et al. 2015) to potentially discriminate the signatures from different metacommunity processes (Fortin & Dale 2005; Rosindell et al. 2012). We use 'traits' in the broad sense to refer to a measurable attribute of an organism (e.g., morphological, behavioral) that influences its performance and functional role in a given environment (Cadotte et al. 2011; Schneider et al. 2019). Traits often provide deeper insights as to how and why species vary through space and time (e.g. McGill et al. 2006; Spasojevic et al. 2014).

Two main approaches have been used to explore the role of traits for helping to infer processes of metacommunity assembly (**Fig. 1**). First, patterns of trait dispersion of co-occurring species have been used to make inferences about the role of interspecific interactions versus habitat filtering in driving patterns of co-occurrence (e.g., Weiher and Keddy 1995; de Bello 2012). A classical view is that species that are more different in some of their traits would be more likely to co-occur (trait divergence) (MacArthur and Levins 1964; Weiher et al. 1998, 2011; Smith et al. 2013). However, species that are more similar to one another (trait convergence) in certain traits can co-occur, for example, due to habitat filtering (Weiher and Keddy 1995), or due to competitive equivalence (Mayfield and Levine 2010). At the metacommunity level, this would result in different patterns of variation of functional strategies across sites relative to variation of taxonomic composition. By comparing patterns of functional variation across sites—hereafter called functional beta diversity (e.g. Villéger et al. 2013; Bishop et al. 2015)—with patterns of taxonomic beta diversity, we can assess whether functional strategies are either under- or over-dispersed (Swenson et al. 2011; Villéger et al. 2012; Smith et al. 2013; Carvalho et al. 2020; Pelicice et al. 2022) (**Fig. 1a**).

The second major approach in examining the intersection of trait-based and metacommunity ecology is to understand the role of traits in the response of metacommunities to environmental variation (e.g. Meynard et al. 2011; Kleyer et al. 2012; Siefert et al. 2012). If different species traits confer advantage in different environments, we would expect strong correlations between species traits and the environment (i.e., trait-environment relationships), and a stronger response of functional diversity to environmental variation relative to taxonomic diversity (Meynard et al. 2011; Siefert et al. 2012; Sagouis et al. 2017) (**Fig. 1b**). Several statistical developments have aimed towards quantifying these trait-environment relationships in order to achieve a better understanding of community assembly (e.g. Dolédec et al. 1996; Kleyer et al. 2012; Brown et al. 2014; Warton et al. 2015; Ovaskainen et al. 2017; ter Braak 2019).

Despite the apparent potential of a trait-based metacommunity ecology, some skepticism has emerged (Clark 2016; Didham et al. 2016). For example, many studies have shown that responses of functional diversity to environmental variation can be weaker than taxonomic responses (e.g. Bishop et al. 2015; Ossola et al. 2015; Carvalho et al. 2020; Saito et al. 2020; Peng et al. 2021; Tison-Rosebery et al. 2022), and the link between a given measured trait and species performance (Shipley et al. 2016) or distribution (Bohner and Diez 2020) is often weak. Indeed, the traditional niche-based perspective is only one mechanism that can influence the co-occurrence of species in a location and their variation along environmental gradients. Other mechanisms, including dispersal limitation, drift, and density-dependence might influence patterns of species traits and their distributions along environmental gradients in a fundamentally different way than expected from a niche-centered perspective (Leibold and Chase 2017). As a consequence, some authors have called for a better use of traits (Bishop et al. 2015; Didham et al. 2016; Schneider et al. 2019; Dawson et al. 2021) or for more trait information to improve the utility of a trait-based metacommunity ecology (McGill et al. 2006; Weiher et al. 2011; Shipley et al. 2016; Sarremejane et al. 2020).

Despite qualitative literature reviews (e.g. McGill et al. 2006; Weiher et al. 2011; Shipley et al. 2016), a quantitative synthesis regarding the role of trait-based approaches in metacommunity ecology is lacking. Here, we compare taxonomic and functional diversity patterns, and their responses to environmental variation across ecosystems, using a global database that was assembled explicitly for the purpose of synthetic analyses on species-trait-environment relationships (CESTES [metaCommunity Ecology: Species, Traits, Environment and Space]) (Jeliazkov et al. 2020). The database consists of 80 datasets from studies on different taxa, ecosystem types, and background conditions from across the world (**Appendix S1**; (Jeliazkov et al. 2020)).

With this dataset compilation, we specifically investigated the following questions:

(1) *When can we infer metacommunity processes from general variation of trait dispersion across communities?* (**Fig. 1a**) Based on null modelling, significant spatial structuring of functional beta diversity relative to taxonomic beta diversity is used to infer potential mechanisms underlying metacommunity structure (i.e., underdispersion due to environmental filtering or overdispersion due to competitive interactions). Alternatively, if functional beta diversity is random with respect to taxonomic beta diversity, we might conclude that the examined traits play little role in helping explain metacommunity patterns (e.g., Swenson et al. 2011; Bishop et al. 2015), or there could be a mixture of over- and under-dispersed functional strategies (Weiher et al. 1998; Chase and Leibold 2003; Mayfield and Levine 2010). We also explored which types of traits (life history, morphology, mobility, etc.) were most likely to help inference.

(2) *Is functional diversity a better indicator of metacommunity response to environmental variation relative to taxonomic diversity?* (**Fig. 1b**) Based on a correlative analysis of functional and taxonomic diversities with environmental variation, the response of functional diversity can be stronger because dispersal limitation and ecological drift of functionally similar species may reduce the response of taxonomic composition to environment (e.g., Ozinga et al. 2005; Weiher et al. 2011). Alternatively, if measured traits do not capture all of the nuance that allows species to persist in a given place, taxonomic diversity may better match the environment than functional diversity (e.g., Bishop et al. 2015; Clark 2016). We examined whether the strength of this relationship was influenced by: (i) level of human disturbance, as traits may reflect how species can cope with these disturbances (e.g., Devictor et al. 2008); (ii) mode of dispersal, which may influence the functional response to variation in environment (e.g. Ozinga et al. 2005); (iii) spatial scale (extent), which can influence the degree of environmental heterogeneity encompassed in the study, and thus the likelihood of environmental matching (Weiher et al. 2011); (iv) sampling properties of the dataset, as variation in the number of traits, species, sites, and environmental variables measured may all affect the detection of trait-environment relationships and the comparison of functional vs. taxonomic diversity responses (Dray and Legendre 2008; Leibold and Chase 2017).

We approached these questions via a synthesis perspective by integrating previously scattered information to address general questions that could not be tested based on single individual datasets. Therefore, our specific aim was not to test specific hypotheses (e.g., which traits are related to which environmental variables) given the wide diversity and heterogeneity among study systems, but rather how trait diversity patterns can generally help infer processes in metacommunity ecology. These predictions are mainly heuristic and do not imply direct causality. Instead, they offer the opportunity to test hypotheses derived from general ecological theories on the mechanisms potentially underlying biodiversity patterns.

Methods

Metacommunities, traits, and environmental data

We used the CESTES database—a global database for metacommunity ecology: species, traits, environment and space (see Jeliazkov et al. 2020)—that was assembled explicitly for the purpose of synthetic analyses on trait-species-environment relationships across taxa, ecosystem types, and scales (**Appendix S1**). In this database, the traits are available at the species level. They were compiled by the authors of the original studies, either from various regional, national or international scientific sources (e.g. trait databases, ecology books, naturalist reports), or sometimes from local field measurements.

Each study analyzed empirical multivariate trait-environment relationships, and publications of datasets ranged from 1996, when the first multivariate study of trait-environment relationships was published (Dolédec et al. 1996) to 2019. Importantly, each study was designed for testing trait-species-environment relationships, and thus datasets were originally sampled and/or assembled explicitly for this purpose (i.e. ensuring environmental and trait variability, relevant traits with respect to environmental conditions under study, balanced trait distributions, complete information; see Jeliazkov et al. 2020). Each dataset included four data matrices: community data (species abundances or presences/absences across multiple sites), species traits, environmental variables across sites, and spatial coordinates (**Appendix S1**). Here, we define a metacommunity in the broad sense as assemblages of species that potentially interact, are distributed across potentially heterogeneous landscapes, and are potentially connected by spatial processes (e.g. dispersal) (Leibold and Chase 2017).

Exploring taxonomic and functional beta diversity patterns

To compare the taxonomic and functional beta diversity of each dataset (**Fig. 1a**), we used Rao's quadratic entropy (Rao 1982) and calculated the normalized version of the proportional beta-equivalent-additive index proposed by de Bello et al. (2010) ("beta_prop") via their 'Rao' function (see calculation details in **Appendix S2a**). This index derives from an additive partitioning of diversity and is interpreted as the average proportional difference between regional and local communities in terms of species composition (taxonomic facet) or trait composition (functional facet).

This approach has five main advantages in the context of our synthesis. First, it can integrate information on species relative abundances. Second, it can be used to calculate any facet of beta diversity (i.e. taxonomic, functional, phylogenetic, etc.) and to compare these facets within the same, standardized framework (de Bello et al. 2010). Third, it can produce uncorrelated indices of functional and taxonomic diversity (Botta-Dukát 2005), which is particularly useful to disentangle these two facets in an equitable comparison. Fourth, as the index scales between 0 and 1, this approach can be used to compare indices across different communities and regions (Chao et al. 2012). Fifth, Rao's quadratic entropy can be used to test trait convergence and divergence (de Bello 2012).

To test our first question, when functional diversity patterns reveal metacommunity assembly processes, we examined the patterns of functional beta diversity independently from the changes in taxonomic diversity by using a null model approach (Schleuter et al. 2010; Swenson et al. 2011). We calculated the observed total Taxonomic Beta Diversity (TBD) and Functional Beta

Diversity (FBD), based on both single and multiple traits, as the proportional beta-equivalent-additive index for each of the 80 datasets (**Appendix S2a**) (de Bello et al. 2010). To produce the null reference of each dataset, we applied an unconstrained trait-shuffling algorithm that permutes species labels across the species trait vector (single-trait) or matrix (multiple-trait) while the species abundance/presence-absence matrix remains unchanged; this was repeated 1000 times. This algorithm ensures that the species abundance/presence-absence matrix keeps the same spatial structure and species richness, while the species-traits links are shuffled. Because the distribution of the beta diversity indices calculated on the null reference data were not distributed normally in most of the cases (71 out of 80 datasets), we log transformed the values of these indices for both the observed and null-based indices (Botta-Dukát 2018). To assess the significance of low vs. high functional turnover, we calculated the Standardized Effect Size on these log transformed values (Swenson 2014) as:

$$SES\ FBD = [\ logFBD_{obs} - mean(logFBD_{null})\ ] \ / \ sd(logFBD_{null})$$

where FBD_{obs} is the observed total Functional Beta Diversity of the dataset, and we used 1000 null reference communities to estimate the mean ($mean(logFBD_{null})$) and standard deviation ($sd(logFBD_{null})$) of the null expected FBD. A SES that is higher than 1.96 is taken to indicate high functional turnover relative to taxonomic turnover, whereas a SES lower than -1.96 is taken to indicate low functional turnover relative to taxonomic turnover (e.g. Swenson et al. 2011). These threshold values correspond to the critical values of a two-sided test with a 0.05 level of significance and a normal distribution centered on zero. A SES between -1.96 and 1.96 is taken to indicate that metacommunity structure is unrelated to the species' trait(s) analyzed.

Although traits cannot be classified into strict categories (e.g. Violle et al. 2007), we used an exploratory exercise to study the ability of different types of traits to reveal significant patterns of functional diversity. Specifically, we classified all the traits of the 80 datasets (i.e. 1084 traits / trait modalities) into nine broad categories (in the same vein as e.g. Dawson et al. 2021; Martini et al. 2021) (**Table 1**; data available at: https://doi.org/10.57745/LLBAZD) and explored the potential relationship between FBD pattern significance and types of traits. We also explored the distribution of the proportion of structuring traits across kingdoms and ecosystems (Dawson et al. 2021), and across study groups as conditioned by the original studies (plant groups were further adjusted from Dansereau's classification of formation-types; Penfound 1967; Whittaker 2012).

Modelling the response of functional and taxonomic beta diversity to environment

To analyze the response of functional and taxonomic beta diversity to environmental variation (**Fig. 1b**), we used the pairwise version of the beta-equivalent-additive index (de Bello et al. 2010). This metric uses the same calculation as the total beta diversity, but instead of the whole metacommunity, one index is calculated for each pair of sites (communities). This results in a site-by-site matrix of beta diversities that reflects pairwise taxonomic (TBDp) or functional (FBDp) beta diversity, respectively (**Appendix S2b**). This allows us to analyze the extent to which environmental differences across sites contribute to these compositional differences within a synthetic context.

To reduce collinearity in the environmental information, we first applied principal component analyses for every dataset ('dudi.pca' and 'dudi.hillsmith' in {ade4}; Dray and Dufour 2007). We kept the principal axes that together explained more than 99% of the total variation of the environmental data. To estimate site-by-site environmental variation, we calculated the

Euclidean distances between sites based on these orthonormal (scaled) predictors (‘dist’ in {stats}; R Core Team 2018).

We analyzed the link between pairwise functional and taxonomic beta diversities, and the environmental distances for each dataset by a regression on distance matrices (Lichstein 2007; Saito et al. 2020). We chose this modelling approach because: (i) it is useful for inferring links between beta diversity variation and environmental variation (e.g. Tuomisto and Ruokolainen 2006); (ii) it is adapted to handle potential non-linear relationships between response and predictor; (iii) it makes no assumption on the underlying distribution of the original variables (Goslee 2009); and (iv) it allows us to use exactly the same number of environmental predictors across all the datasets, namely one compound matrix of environmental distances that synthesizes the overall variability of the environment across the sites. We used a Generalized Additive Model (GAM) with a spline-based smoothing parameter allowing three knots (k=3; ‘gam’ in {mgcv}; Wood 2011) to detect potential hump-shaped relationships that may exist between compositional and environmental distances (e.g., Ferrier et al. 2007) while avoiding convergence issues for some datasets with small sample size.

First, to assess how well the environmental variation explained TBDp and FBDp variations, we calculated the R^2 of the two models for every dataset; R^2_{TBDp}, and R^2_{FBDp}, respectively. Note that the R^2 values returned by distance-based approaches are systematically lower than by raw-data based approaches due to the derived nature of distances (Goslee 2009, Legendre and Fortin 2010, Legendre and Legendre 2012). Thus, they should only be considered in relation to each other across datasets. We then compared the size of R^2_{TBDp} relative to R^2_{FBDp} for every dataset. We finally calculated the relative sensitivity of FBDp to environmental variations as the difference between R^2_{FBDp}, and R^2_{TBDp}. A FBDp relative sensitivity of zero means that the functional beta diversity is as sensitive to environment as taxonomic beta diversity, while as FBDp rises higher above 0, the sensitivity of functional beta diversity to environment relative to taxonomic beta diversity increases (**Fig. 1b**).

To assess the differences of sensitivity of functional beta diversity to environment across ecosystems, scales, and sampling properties, we modeled the response of FBDp relative sensitivity in response to three predictors and their interactions: the level of human disturbance (levels: Natural, Mixed, Disturbed), the dispersal mode of the group (levels: Sessile, Swimmers, Walkers, Flyers), and the spatial extent of the study (log transformed). We included three general sampling properties as additional predictors: the number of environmental variables, the sample size, and the trade-off between number of traits and number of species (see **Appendix S3**). To build this model, we used a Bayesian Generalized Linear Multilevel Model (‘brm’ in {brms}; Bürkner 2017) with a Gaussian family and non-informative priors (uniform distribution) on the coefficients of the predictors. We checked the balance of our factorial design by data visualization (**Appendix S4**) and scaled the numeric predictors to facilitate the interpretation of their relative contribution to the FBDp relative sensitivity. Some datasets that were temporal replicates of a given sampling were considered as part of the same study. We thus added the study identifier as a random effect in the model to account for the potential dependence between the datasets that belonged to the same study (**Table S1.1**). We checked the model convergence and parameters estimation by examining the trace and density plots for Markov Chain Monte Carlo draws (‘traceplot’ function).

To verify the influence of the method choice on our conclusions, we complemented the above analysis focused on trait dispersion, with other trait-based approaches that focus on trait composition variation explained by environment (double-CCA; ter Braak et al. 2018) and individual trait-environment relationships (fourth-corner & RLQ; Dray et al. 2014) and that are able to keep an equitable comparison (i.e. independence) between taxonomical and functional response to environment (hence excluding the Community Weighted Means approach that integrates taxonomy-related information, see Peres-Neto et al. 2017; Zelený 2017, 2018; **Appendices S5-S7**).

Twelve datasets out of 80 only had presences/absences, not abundances, but were treated with the same methods as the others since it did not compromise our overall aim of comparing taxonomic with functional response in relative terms. In the synthesis analysis, we accounted for the potential effect of this difference through the random effect applied on the study identifier.

We performed all analyses in R (R Core Team 2021) and all scripts and files are available at: https://doi.org/10.57745/LLBAZD.

Results

Inferences from patterns of functional beta diversity

When we used multi-trait functional diversity, we found that only 20/80 (25%) datasets showed a significant structure in the dispersion of functional strategies between sites (**Fig. 2a**). Among these 20 datasets, 15 datasets indicate trait divergence and 5 datasets indicate trait convergence.

When we used single-trait functional diversity, we found that up to 47 out of the 80 datasets include at least one trait that revealed significant trait dispersion, mostly as trait divergence (**Fig. 2a**), particularly in plants, aquatic invertebrates and terrestrial insects (**Fig. 2b**). However, on average, only 19% (min=0%, 1st quartile=0%, 2nd quartile=7%, 3rd quartile=29%, max=100%) of the trait information included in a given dataset showed any significant pattern (**Appendix S7**). This proportion varied across some study groups, but not across kingdoms (Plantae vs. Animalia;

Kruskal-Wallis chi-squared = 3.5201, df = 3, p-value = 0.3182; **Fig. 2c**) nor ecosystem types (Kruskal-Wallis chi-squared = 2.6833, df = 2, p-value = 0.2614; **Fig. 2d**).

The metacommunities showing mostly random trait patterns here were not necessarily the ones with strongest signals of dispersal limitation (**Appendix S8**).

We found that all categories of traits can show either trait divergence or convergence (**Fig. 3a**). Marginally, traits related to species status, life history, mobility, and integrative, unclassifiable traits (e.g. competitive strategy, survival, productivity), had a proportionately higher propensity to have underlying structure than traits related to habitat preference or morphology (**Fig. 3b**). Thus, the categories of traits that have the most data (e.g. body- or feeding-related traits), are not necessarily the ones with the most signal (**Fig. 3**).

Sensitivity of taxonomic vs. functional beta diversity to environment

In most instances, we found that pairwise taxonomic beta diversity was better explained by the environment than was pairwise functional beta diversity (**Fig. 4a**). That is, 61 out of the 80 datasets (76%) showed a negative relative sensitivity of functional beta diversity to environment (**Fig. 4b**), indicating that taxonomic beta diversity is slightly more sensitive to environment than functional beta diversity (Wilcoxon paired test, W=2397, PV=0.003).

Even after considering different ways of analyzing the data, the results remain consistent (**Appendices S5, 6, 9**). For instance, according to the RLQ analysis, 36% of the datasets showed a general significant link between traits and environment, while 75% was between species and environment (**Fig. S6.1**). Likewise, from the double-CCA analysis, on average, only 33% of the species composition that was explained by the environment was potentially due to their traits (**Fig. S5.1**).

Overall, the sampling properties (e.g., number of traits, sample size) tested in our meta-analysis had a relationship with the relative sensitivity of the pairwise functional beta diversity, whereas the ecological factors had no or only weak relationships (**Fig. 5; Appendices S11-12**). The increase of the number of traits relative to the number of species had a positive link with the functional beta diversity relative sensitivity (**Fig. 5a**; **Fig. S11.1a**). Regarding the ecological factors, we observed only one marginal interaction involving the dispersal mode and the level of disturbance (**Fig. 5b**). Specifically, the sensitivity of functional beta diversity to environmental variation for metacommunities that were categorized as 'Walkers' was higher in more disturbed systems (**Fig. 5b**; **Fig. S11.1b**).

Discussion

Inferences from patterns of functional beta diversity

Among the 80 datasets analyzed here, we showed that functional diversity enhanced our ability to inferring metacommunity processes in only 25% of the datasets using a multi-trait approach, but up to 59% using a single-trait approach (with on average 19% of the traits showing significant dispersion). This relatively small proportion of studies does not necessarily mean that competitive interactions or environmental filtering are not important in these systems, but rather that we are not able to detect them with the traits measured and the null modelling approach traditionally used to study trait diversity across metacommunities (as observed elsewhere; Thompson et al. 2010; Bishop et al. 2015; Carvalho et al. 2020; Pelicice et al. 2022). While the approach based on single traits seems to be almost twice more performant than the multi-trait approach in unravelling metacommunity processes (in line with e.g. Weiher et al. 1998; Lepš et al. 2006), we suspect that only a small proportion of the measured traits may actually be relevant to this specific aim.

There are several reasons why we might not have detected strong trait dispersion even if important trait-mediated interactions are taking place. For example, when multiple traits are considered, we might simultaneously expect convergence of some traits and divergence of others (Weiher et al. 1998; Chase and Leibold 2003; Mayfield and Levine 2010), depending on the scale of analysis (Algar et al. 2011). These opposite responses could lead to the overall neutral effect that we observed in most studies (mixture in **Fig. 1**). However, the single-trait analysis does not systematically support this hypothesis because only 9/60 datasets that showed a random multi-trait turnover had signals of both convergence and divergence. Because most single trait analyses support both divergence and convergence patterns, this again emphasizes the limitations of such analyses for disentangling metacommunity processes across scales. In this case, a more complete solution would be to formulate different expectations for each trait and each scale (e.g. local vs. regional) (de Bello et al. 2009; Gianuca et al. 2017; Escobedo et al. 2021).

Even if we could be confident about expectations from different traits, it is also important to recognize general limitations of the null modelling approach we used here (de Bello 2012; Götzenberger et al. 2016). To achieve comparability across datasets, we used the most commonly used unconstrained trait randomization algorithm (Swenson 2014). However, this algorithm might be too conservative to test the functional link between species (de Bello 2012). Instead, it might be more appropriate to use several null-models (e.g., de Bello et al. 2009; de Bello 2012; Chalmandrier et al. 2013; Götzenberger et al. 2016), accounting for the regional species pool structure (de Bello et al. 2010; de Bello 2012), or to develop more permissive null models, as done when analyzing phylogenetic diversity patterns (e.g. Hardy 2008). However, many of the parameters needed for these sorts of null models (e.g., specification of the regional species pool) are not readily available for a synthetic analysis across studies, and the challenge remains to develop null models adapted to studying functional beta diversity patterns (de Bello 2012). It is also important to recall that this study does not allow us to draw direct causal links between patterns and processes, but instead provides insights on the potential existence of such links and allows us to assess the added value of functional information.

Another limitation of the studies we synthesized could be if some study designs were underpowered (e.g. small sample size or number of traits in some datasets). However, (i) the vast majority of the CESTES datasets are appropriate for trait-environment analyses (see Figure 6 in Jeliazkov et al. 2020); (ii) we compared taxonomic with functional diversity all else (including biases) being equal in terms of sample size and site conditions; (iii) we showed that our results were insensitive to sample size and sensitive to number of traits relative to number of species (**Appendix S13**).

Despite the limitations of analyses of functional turnover patterns, the results of our synthesis show that multi-trait approaches with species-level traits rarely allow us to draw inference about the mechanisms potentially underlying metacommunity structure. First, it is possible that metacommunity patterns are largely neutral with respect to the functional traits measured. In principle, dispersal limitation and neutrality could structure most of these metacommunities and leave a stronger signature in the spatial variation of taxonomic composition than that of trait composition (Swenson et al. 2011; de Bello et al. 2013). However, our analyses indicate that the random trait dispersion often observed in the datasets analyzed here is less likely the sign of dispersal limitation than of the difficulty in capturing metacommunity complexity (**Appendix S9**). It is also possible that the threshold of species distinctiveness in the functional trait space, and the order of diversity (i.e., how species are weighted in proportion to their relative abundances) that are used to calculate the functional diversity may influence our ability to draw inference (Chao et al. 2019; **Appendix S10**).

Overall, we found that the limits of these trait-based approaches in inferring metacommunity processes may be general across systems (**Appendix S13**). Although outcomes are highly contingent on the way one groups the datasets (Dawson et al. 2021; **Appendix S8**), we did detect more frequent signatures of trait divergence among plants than in other groups. Whether this is due to fundamental differences in metacommunity dynamics, or in trait relevancy, remains an open question.

Interestingly, we detected both convergence and divergence of traits among all trait categories, which complicates the challenge of choosing specific traits to test specific hypothesis. A marginal exception may be the traits related to species status (distribution, rarity, etc.) that seem more relevant to test hypotheses on limiting similarity across scales, probably because they best reflect species abundance variation and thus species' niches or fitness (McGill et al. 2006; Shipley et al. 2016). Despite the exploratory nature of this trait grouping analysis, we note that species' mobility characteristics may be better predictors of metacommunity structuring across space than habitat preferences. This may be due to the potentially strong influence of dispersal limitation in many of these metacommunities (**Appendix S9**). This supports the idea that integrating species' dispersal ability and mobility will help improve trait-based approaches for inference in metacommunity ecology (Leibold and Chase 2017), provided appropriate null modelling is used (de Bello 2012; Götzenberger et al. 2016). Finally, we note that more integrative traits (e.g. species status, composite traits) may be more useful to unravelling metacommunity processes.

Sensitivity of taxonomic vs. functional beta diversity to environment

As with our first analysis, the use of traits provided little improvement for our ability to predict metacommunity response to environment compared to analyses using taxonomy alone, despite the fact that environmental context was explicitly informed. Importantly, these conclusions held even after considering different ways of analyzing the data (summarized in **Appendix S5**), and were in concordance with syntheses on stream mayflies (Saito et al. 2020) and plants (Bruelheide et al. 2018). A first reason for this may be that the traits were inappropriately chosen with respect to the environment (e.g. Bishop et al. 2015; Ossola et al. 2015). This may be due to a weak link between the traits used and the demographic rates and species performance in a given environment (McGill et al. 2006; Violle et al. 2007; Weiher et al. 2011; Shipley et al. 2016).

We showed that the low sensitivity of functional beta diversity to environment is generalizable across ecosystem types, taxonomic groups, dispersal modes, and scales, despite some specific combinations of ecological situations and sampling contexts. However, when we use more traits relative to the number of species functional beta diversity becomes more sensitive to the environment, probably due to a subsequent decrease in functional redundancy (**Appendix S11: Fig. S11.4**). This is also consistent with the idea that taxonomic diversity may encompass more of the complexity of metacommunity responses than does functional diversity (Clark 2016) (see also **Appendix S10**).

The importance of trait variation within species, and how it may influence expected patterns, remains an open question (e.g., Violle et al. 2012; Guisan et al. 2019). Ignoring trait variation within species across habitats could certainly have influenced our observed weak responses of communities to environmental variation (Bolnick et al. 2011; de Bello et al. 2011; Swenson et al. 2011). While integrating trait variation can increase predictability (e.g., Albert et al. 2011; de

Bello et al. 2011), it is still unclear how much we would gain from functional information measured at the individual level compared to the taxonomy alone (Clark 2016; Read et al. 2017), and in which contexts (i.e. taxon, type of traits or gradient, study scale, etc.; Albert et al. 2011; de Bello et al. 2011; Siefert et al. 2015). At intermediate scales, where the majority of our analyses took place, reducing biological complexity down to a few functional traits may not always refine our understanding of community structure (in line with de Bello et al. 2013; Escobedo et al. 2021).

Conclusions and prospects for future research directions

More than 15 years after Violle et al.'s (2007) call—"Let the concept of trait be functional!"—and following an intense discussion on the utility of traits in (meta)community ecology (see e.g., Didham et al. 2016 vs. Shipley et al. 2016), we here provide a synthesis of empirical evidence regarding the contribution of traits and their diversity for understanding metacommunity structure when compared to taxonomic diversity alone. We expected to find evidence that traits play an important role in mediating our understanding and inference of metacommunity processes across different groups (Keddy 1992; McGill et al. 2006; Mouillot et al. 2013; Cadotte et al. 2015). However, results from our synthesis confirm recent concerns (Didham et al. 2016) regarding the limitations of trait-based approaches in metacommunity ecology. Despite some exceptions (many of which we discuss here), our overall results suggest that species-level traits may rarely bring predictive advantages over what the taxonomic information already holds. We explored the potential of two main approaches (and several more, see Supp. Mat.) used to infer potential metacommunity processes, namely (i) testing functional diversity patterns against null models, and (ii) comparing how functional diversity responds to environmental variation compared with taxonomic diversity. We found that although the second approach involves more information (measure of environmental heterogeneity), it brought even less insight than the former, possibly because of an overall high influence of dispersal in these metacommunities (e.g. Heino et al. 2015). The best practice for single datasets would be to refine the null model based on the environmental and spatial information available and to assess the trait structuring across environmental gradients (e.g. de Bello 2012; de Bello et al. 2013; Escobedo et al. 2021), and scales (e.g. Gianuca et al. 2017). In a synthesis context though, one would face the challenge of keeping this strategy comparably efficient across all datasets.

Analyses in some systems have shown the benefit of traits in predicting community response to environment (e.g. Meynard et al. 2011; Mouillot et al. 2013; Abonyi et al. 2018), whereas others show (e.g. Clark 2016; Read et al. 2017; Saito et al. 2020) that taxonomic information is richer and better respond to environment than functional information. Our synthesis shows that overall, these traits or functional groups could rarely be used as a surrogate of metacommunity response to environment. Given the substantial influence of environment on these metacommunities, we thus question the ability of the currently available traits to capture the complexity of community-environment relationships.

We suggest several refinements for improving trait-based analyses of metacommunities, including (i) searching for traits that reflect the demographic rates and performance associated with population-level processes as more direct measures of species responses to each other and the environment (Weiher et al. 2011; Shipley et al. 2016), (ii) incorporating the rich and varied way that traits can influence species composition in natural metacommunities, such as phenology, biotic interactions, and dispersal (see e.g. Sarremejane et al. 2020; Bernard et al. 2023), (iii) considering scale-explicit approaches to study the role of different traits in metacommunity dynamics depending on disturbance, scales (e.g. Smith et al. 2013; Mazel et al. 2014; Carmona et al. 2016; Perronne et al. 2017; Escobedo et al. 2021), and alpha, beta and gamma diversity components (Spasojevic et al. 2014; Gianuca et al. 2017), (iv) using complementary and customized null modelling approaches (e.g. de Bello 2012; Ford and Roberts 2020), and (v) integrating the potential habitat connectivity into the analysis of trait dispersion using network analyses (e.g. Layeghifard et al. 2015).

Powerful process-based frameworks have also been developed to predict plant metacommunity assembly based on functional traits (Lavorel and Garnier 2002; Laughlin et al. 2012), mainly associated with niche-based processes. We should develop these approaches further so that they can empirically apply to other groups and to a more comprehensive range of questions that are currently challenging the field of metacommunity ecology by accounting for both spatial and temporal variation (Webb et al. 2010; García-Girón et al. 2019), and for scale-dependence (Smith et al. 2013; Wang et al. 2013). This would help us to assess the relative role of traits in metacommunity dynamics and further clarify the mechanistic links between traits and metacommunity processes.

Acknowledgments

We thank S. Chantepie and P. Keil for invaluable advices on the analyses; C. ter Braak, S. Dray, and M. Kleyer for discussions on the methods; the data providers who contributed to the CESTES database; F. de Bello and four Reviewers for their constructive and helpful comments on different versions of this manuscript. This work was funded by the German Centre for Integrative Biodiversity Research (iDiv) Halle- Jena- Leipzig (funded by the German Research Foundation; DFG FZT 118, 202548816).

Statement of Authorship

Conceptualization: JMC & AJ; Data Curation: AJ; Formal Analysis: AJ; Funding acquisition: JMC; Investigation: AJ & JMC; Methodology: AJ; Software: AJ; Project Administration: AJ & JMC; Supervision: JMC; Validation: AJ; Visualization: AJ; Writing – Original Draft Preparation: AJ; Writing – Review & Editing: AJ & JMC.

Data and Code Accessibility

All the data used for this study – the CESTES datasets – are published, publicly available and archived according to open data requirements at: https://idata.idiv.de/ddm/Data/ShowData/286 (Jeliazkov and the CESTES consortium 2019).

Additional formats of the CESTES data and all of the R scripts used for this study are available at: https://doi.org/10.57745/LLBAZD (Jeliazkov 2023).

Literature cited

Abonyi, A., Z. Horváth, and R. Ptacnik. 2018. Functional richness outperforms taxonomic richness in predicting ecosystem functioning in natural phytoplankton communities. Freshwater Biology 63:178–186.

Albert, C. H., F. Grassein, F. M. Schurr, G. Vieilledent, and C. Violle. 2011. When and how should intraspecific variability be considered in trait-based plant ecology? Perspectives in Plant Ecology, Evolution and Systematics 13:217–225.

Algar, A. C., J. T. Kerr, and D. J. Currie. 2011. Quantifying the importance of regional and local filters for community trait structure in tropical and temperate zones. Ecology 92:903–914.

Bernard, C., G. S. Santos, J. A. Deere, R. Rodriguez-Caro, P. Capdevila, E. Kusch, S. J. L. Gascoigne, et al. 2023. MOSAIC – A Unified Trait Database to Complement Structured Population Models. Scientific Data 10:335.

Bishop, T. R., M. P. Robertson, B. J. Rensburg, and C. L. Parr. 2015. Contrasting species and functional beta diversity in montane ant assemblages. Journal of Biogeography 42:1776–1786.

Bohner, T., and J. Diez. 2020. Extensive mismatches between species distributions and performance and their relationship to functional traits. Ecology Letters 23:33–44.

Bolnick, D. I., P. Amarasekare, M. S. Araújo, R. Bürger, J. M. Levine, M. Novak, V. H. W. Rudolf, et al. 2011. Why intraspecific trait variation matters in community ecology. Trends in Ecology & Evolution 26:183–192.

Botta-Dukát, Z. 2005. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. Journal of Vegetation Science 16:533–540.

Botta-Dukát, Z. 2018. Cautionary note on calculating standardized effect size (SES) in randomization test. Community Ecology 19:77–83.

Brown, A. M., D. I. Warton, N. R. Andrew, M. Binns, G. Cassis, and H. Gibb. 2014. The fourth-corner solution – using predictive models to understand how species traits interact with the environment. Methods in Ecology and Evolution 5:344–352.

Bruelheide, H., J. Dengler, O. Purschke, J. Lenoir, B. Jiménez-Alfaro, S. M. Hennekens, Z. Botta-Dukát, et al. 2018. Global trait–environment relationships of plant communities. Nature Ecology & Evolution 2:1906–1917.

Bürkner, P.-C. 2017. brms: An R Package for Bayesian Multilevel Models Using Stan. Journal of Statistical Software 80:1–28.

Cadotte, M. W., C. A. Arnillas, S. W. Livingstone, and S.-L. E. Yasui. 2015. Predicting communities from functional traits. Trends in Ecology & Evolution 30:510–511.

Cadotte, M. W., K. Carscadden, and N. Mirotchnick. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. Journal of Applied Ecology 48:1079–1087.

Carmona, C. P., F. de Bello, N. W. H. Mason, and J. Lepš. 2016. Traits Without Borders: Integrating Functional Diversity Across Scales. Trends in Ecology & Evolution 31:382–394.

Carvalho, J. C., J. Malumbres-Olarte, M. A. Arnedo, L. C. Crespo, M. Domenech, and P. Cardoso. 2020. Taxonomic divergence and functional convergence in Iberian spider forest communities: Insights from beta diversity partitioning. Journal of Biogeography 47:288–300.

Chalmandrier, L., T. Müunkemüller, L. Gallien, F. de Bello, F. Mazel, S. Lavergne, and W. Thuiller. 2013. A family of null models to distinguish between environmental filtering and biotic interactions in functional diversity patterns. Journal of vegetation science : official organ of the International Association for Vegetation Science 24:853–864.

Chao, A., C.-H. Chiu, and T. C. Hsieh. 2012. Proposing a resolution to debates on diversity partitioning. Ecology 93:2037–2051.

Chao, A., C.-H. Chiu, S. Villéger, I.-F. Sun, S. Thorn, Y.-C. Lin, J.-M. Chiang, et al. 2019. An attribute-diversity approach to functional diversity, functional beta diversity, and related (dis)similarity measures. Ecological Monographs 89:e01343.

Chase, J. M., A. Jeliazkov, E. Ladouceur, and D. S. Viana. 2020. Biodiversity conservation through the lens of metacommunity ecology. Annals of the New York Academy of Sciences 1469:86–104.

Chase, J. M., N. J. B. Kraft, K. G. Smith, M. Vellend, and B. D. Inouye. 2011. Using null models to disentangle variation in community dissimilarity from variation in α-diversity. Ecosphere 2:art24.

Chase, J. M., and M. A. Leibold. 2003. Ecological Niches: Linking Classical and Contemporary Approaches. University of Chicago Press.

Chase, J. M., and J. A. Myers. 2011. Disentangling the importance of ecological niches from stochastic processes across scales. Philosophical Transactions of the Royal Society B: Biological Sciences 366:2351–2363.

Clark, J. S. 2016. Why species tell more about traits than traits about species: predictive analysis. Ecology 97:1979–1993.

Cottenie, K. 2005. Integrating environmental and spatial processes in ecological community dynamics. Ecology Letters 8:1175–1182.

Dawson, S. K., C. P. Carmona, M. González-Suárez, M. Jönsson, F. Chichorro, M. Mallen-Cooper, Y. Melero, et al. 2021. The traits of "trait ecologists": An analysis of the use of trait and functional trait terminology. Ecology and Evolution 11:16434–16445.

de Bello, F. 2012. The quest for trait convergence and divergence in community assembly: are null-models the magic wand? Global Ecology and Biogeography 21:312–317.

de Bello, F., S. Lavergne, C. N. Meynard, J. Lepš, and W. Thuiller. 2010. The partitioning of diversity: showing Theseus a way out of the labyrinth. Journal of Vegetation Science 21:992–1000.

de Bello, F., S. Lavorel, C. H. Albert, W. Thuiller, K. Grigulis, J. Dolezal, Š. Janeček, et al. 2011. Quantifying the relevance of intraspecific trait variability for functional diversity. Methods in Ecology and Evolution 2:163–174.

de Bello, F., W. Thuiller, J. Lepš, P. Choler, J. Clément, P. Macek, M. Sebastià, et al. 2009. Partitioning of functional diversity reveals the scale and extent of trait convergence and divergence. Journal of Vegetation Science 20:475–486.

de Bello, F., M. Vandewalle, T. Reitalu, J. Lepš, H. C. Prentice, S. Lavorel, and M. T. Sykes. 2013. Evidence for scale- and disturbance-dependent trait assembly patterns in dry semi-natural grasslands. Journal of Ecology 101:1237–1244.

Devictor, V., R. Julliard, J. Clavel, F. Jiguet, A. Lee, and D. Couvet. 2008. Functional biotic homogenization of bird communities in disturbed landscapes. Global Ecology and Biogeography 17:252–261.

Didham, R. K., S. R. Leather, and Y. Basset. 2016. Circle the bandwagons – challenges mount against the theoretical foundations of applied functional trait and ecosystem service research. Insect Conservation and Diversity 9:1–3.

Dolédec, S., D. Chessel, C. J. F. ter Braak, and S. Champely. 1996. Matching species traits to environmental variables: a new three-table ordination method. Environmental and Ecological Statistics 3:143–166.

Dray, S., P. Choler, S. Dolédec, P. R. Peres-Neto, W. Thuiller, S. Pavoine, and C. J. F. ter Braak. 2014. Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. Ecology 95:14–21.

Dray, S., and A.-B. Dufour. 2007. The ade4 package: implementing the duality diagram for ecologists. Journal of Statistical Software 1–20.

Dray, S., and P. Legendre. 2008. Testing the Species Traits–Environment Relationships: The Fourth-Corner Problem Revisited. Ecology 89:3400–3412.

Escobedo, V. M., R. S. Rios, Y. Alcayaga-Olivares, and E. Gianoli. 2021. Disturbance reinforces community assembly processes differentially across spatial scales. Annals of Botany 127:175–189.

Ferrier, S., G. Manion, J. Elith, and K. Richardson. 2007. Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. Diversity and Distributions 13:252–264.

Ford, B. M., and J. D. Roberts. 2020. Functional traits reveal the presence and nature of multiple processes in the assembly of marine fish communities. Oecologia 192:143–154.

García-Girón, J., M. Wilkes, M. Fernández-Aláez, and C. Fernández-Aláez. 2019. Processes structuring macrophyte metacommunities in Mediterranean ponds: Combining novel methods to disentangle the role of dispersal limitation, species sorting and spatial scales. Journal of Biogeography 46:646–656.

Gianuca, A. T., S. A. J. Declerck, M. W. Cadotte, C. Souffreau, T. D. Bie, and L. D. Meester. 2017. Integrating trait and phylogenetic distances to assess scale-dependent community assembly processes. Ecography 40:742–752.

Gilbert, B., and J. R. Bennett. 2010. Partitioning variation in ecological communities: do the numbers add up? Journal of Applied Ecology 47:1071–1082.

Goslee, S. C. 2009. Correlation analysis of dissimilarity matrices. Plant Ecology 206:279–286.

Götzenberger, L., Z. Botta- Dukát, J. Lepš, M. Pärtel, M. Zobel, and F. de Bello. 2016. Which randomizations detect convergence and divergence in trait-based community assembly? A test of commonly used null models. Journal of Vegetation Science 27:1275–1287.

Guisan, A., H. K. Mod, D. Scherrer, T. Münkemüller, J. Pottier, J. M. Alexander, and M. D’Amen. 2019. Scaling the linkage between environmental niches and functional traits for improved spatial predictions of biological communities. (A. Hampe, ed.)Global Ecology and Biogeography geb.12967.

Guzman, L. M., P. L. Thompson, D. S. Viana, B. Vanschoenwinkel, Z. Horváth, R. Ptacnik, A. Jeliazkov, et al. 2022. Accounting for temporal change in multiple biodiversity patterns improves the inference of metacommunity processes. Ecology 103:e3683.

Hardy, O. J. 2008. Testing the spatial phylogenetic structure of local communities: statistical performances of different null models and test statistics on a locally neutral community. Journal of Ecology 96:914–926.

Heino, J., A. S. Melo, and L. M. Bini. 2015. Reconceptualising the beta diversity-environmental heterogeneity relationship in running water systems. Freshwater Biology 60:223–235.

Jeliazkov, A. and the CESTES consortium. 2019. A global database for metaCommunity Ecology: Species, Traits, Environment and Space – version 1.0 (CESTES v1.0). iDiv Biodiversity Portal, https://doi.org/10.25829/idiv.286-21-2695.

Jeliazkov, A., D. Mijatovic, S. Chantepie, N. Andrew, R. Arlettaz, L. Barbaro, N. Barsoum, et al. 2020. A global database for metacommunity ecology, integrating species, traits, environment and space. Scientific Data 7:1–15.

Jeliazkov, A. 2023. Data and R codes for a global synthetic analysis of the role of species traits in inference in metacommunity ecology, V1, Recherche Data Gouv, https://doi.org/10.57745/LLBAZD.

Keddy, P. A. 1992. Assembly and response rules: two goals for predictive community ecology. Journal of Vegetation Science 3:157–164.

Kleyer, M., S. Dray, F. de Bello, J. Lepš, R. J. Pakeman, B. Strauss, W. Thuiller, et al. 2012. Assessing species and community functional responses to environmental gradients: which multivariate methods? (O. Wildi, ed.)Journal of Vegetation Science 23:805–821.

Laughlin, D. C., C. Joshi, P. M. van Bodegom, Z. A. Bastow, and P. Z. Fulé. 2012. A predictive model of community assembly that incorporates intraspecific trait variation. Ecology Letters 15:1291–1299.

Lavorel, S., and E. Garnier. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Functional Ecology 16:545–556.

Layeghifard, M., V. Makarenkov, and P. R. Peres- Neto. 2015. Spatial and species compositional networks for inferring connectivity patterns in ecological communities. Global Ecology and Biogeography 24:718–727.

Legendre, P., and M.-J. Fortin. 2010. Comparison of the Mantel test and alternative approaches for detecting complex multivariate relationships in the spatial analysis of genetic data. Molecular Ecology Resources 10:831–844.

Legendre, P., and L. F. Legendre. 2012. Numerical ecology (Vol. 24). Elsevier.

Legendre, P., X. Mi, H. Ren, K. Ma, M. Yu, I.-F. Sun, and F. He. 2009. Partitioning beta diversity in a subtropical broad-leaved forest of China. Ecology 90:663–674.

Leibold, M. A., and J. M. Chase. 2017. Metacommunity Ecology. Monographs in population biology. Princeton University Press.

Lepš, J., F. De Bello, S. Lavorel, and S. Berman. 2006. Quantifying and interpreting functional diversity of natural communities: practical considerations matter. Preslia 78:481–501.

Lichstein, J. W. 2007. Multiple regression on distance matrices: a multivariate spatial analysis tool. Plant Ecology 188:117–131.

MacArthur, R., and R. Levins. 1964. Competition, habitat selection, and character displacement in a patchy environment. Proceedings of the National Academy of Sciences of the United States of America 51:1207–1210.

Martini, S., F. Larras, A. Boyé, E. Faure, N. Aberle, P. Archambault, L. Bacouillard, et al. 2021. Functional trait-based approaches as a common framework for aquatic ecologists. Limnology and Oceanography 66:965–994.

Mayfield, M. M., and J. M. Levine. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities: Phylogeny and coexistence. Ecology Letters 13:1085–1093.

Mazel, F., F. Guilhaumon, N. Mouquet, V. Devictor, D. Gravel, J. Renaud, M. V. Cianciaruso, et al. 2014. Multifaceted diversity-area relationships reveal global hotspots of mammalian species, trait and lineage diversity. Global ecology and biogeography : a journal of macroecology 23:836–847.

McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. Trends in Ecology & Evolution 21:178–185.

Meynard, C. N., V. Devictor, D. Mouillot, W. Thuiller, F. Jiguet, and N. Mouquet. 2011. Beyond taxonomic diversity patterns: how do α, β and γ components of bird functional and phylogenetic diversity respond to environmental gradients across France? Global Ecology and Biogeography 20:893–903.

Mori, A. S., F. Isbell, and R. Seidl. 2018. β-Diversity, Community Assembly, and Ecosystem Functioning. Trends in Ecology & Evolution 33:549–564.

Mouillot, D., N. A. J. Graham, S. Villéger, N. W. H. Mason, and D. R. Bellwood. 2013. A functional approach reveals community responses to disturbances. Trends in Ecology & Evolution 28:167–177.

Ossola, A., M. A. Nash, F. J. Christie, A. K. Hahs, and S. J. Livesley. 2015. Urban habitat complexity affects species richness but not environmental filtering of morphologically-diverse ants. PeerJ 3:e1356.

Ovaskainen, O., J. Rybicki, and N. Abrego. 2019. What can observational data reveal about metacommunity processes? Ecography 42:1877–1886.

Ovaskainen, O., G. Tikhonov, A. Norberg, F. Guillaume Blanchet, L. Duan, D. Dunson, T. Roslin, et al. 2017. How to make more out of community data? A conceptual framework and its implementation as models and software. Ecology Letters 20:561–576.

Ozinga, W. A., J. H. J. Schaminée, R. M. Bekker, S. Bonn, P. Poschlod, O. Tackenberg, J. Bakker, et al. 2005. Predictability of plant species composition from environmental conditions is constrained by dispersal limitation. Oikos 108:555–561.

Pelicice, F. M., L. da Silva Damasceno, E. de Almeida Ferreira, W. J. da Graça, C. S. Agostinho, and R. Fernandes. 2022. Contrasting continental patterns and drivers of taxonomic and functional turnover among fish assemblages across Brazilian reservoirs. Hydrobiologia 849:373–384.

Penfound, W. T. 1967. A Physiognomic Classification of Vegetation in Conterminous United States. Botanical Review 33:289–326.

Peng, F.-J., C. J. F. ter Braak, A. Rico, and P. J. Van den Brink. 2021. Double constrained ordination for assessing biological trait responses to multiple stressors: A case study with benthic macroinvertebrate communities. Science of The Total Environment 754:142171.

Peres-Neto, P. R., S. Dray, and C. J. F. ter Braak. 2017. Linking trait variation to the environment: critical issues with community-weighted mean correlation resolved by the fourth-corner approach. Ecography 40:806–816.

Peres-Neto, P. R., P. Legendre, S. Dray, and D. Borcard. 2006. Variation Partitioning of Species Data Matrices: Estimation and Comparison of Fractions. Ecology 87:2614–2625.

Perronne, R., F. Munoz, B. Borgy, X. Reboud, and S. Gaba. 2017. How to design trait-based analyses of community assembly mechanisms: Insights and guidelines from a literature review. Perspectives in Plant Ecology, Evolution and Systematics 25:29–44.

R Core Team. 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

———. 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rao, C. R. 1982. Diversity and dissimilarity coefficients: A unified approach. Theoretical Population Biology 21:24–43.

Read, Q. D., J. A. Henning, and N. J. Sanders. 2017. Intraspecific variation in traits reduces ability of trait-based models to predict community structure. (N. Mason, ed.)Journal of Vegetation Science 28:1070–1081.

Ruhí, A., T. Datry, and J. L. Sabo. 2017. Interpreting beta-diversity components over time to conserve metacommunities in highly dynamic ecosystems. Conservation Biology 31:1459–1468.

Sagouis, A., F. Jabot, and C. Argillier. 2017. Taxonomic versus functional diversity metrics: how do fish communities respond to anthropogenic stressors in reservoirs? Ecology of Freshwater Fish 26:621–635.

Saito, V. S., T. Siqueira, L. M. Bini, R. Costa-Pereira, E. P. Santos, and S. Pavoine. 2020. Comparing taxon- and trait-environment relationships in stream communities. Ecological Indicators 117:106625.

Sarremejane, R., N. Cid, R. Stubbington, T. Datry, M. Alp, M. Cañedo-Argüelles, A. Cordero-Rivera, et al. 2020. DISPERSE, a trait database to assess the dispersal potential of European aquatic macroinvertebrates. Scientific Data 7:386.

Schleuter, D., M. Daufresne, F. Massol, and C. Argillier. 2010. A user's guide to functional diversity indices. Ecological Monographs 80:469–484.

Schneider, F. D., D. Fichtmueller, M. M. Gossner, A. Güntsch, M. Jochum, B. König-Ries, G. Le Provost, et al. 2019. Towards an ecological trait-data standard. Methods in Ecology and Evolution 10:2006–2019.

Shipley, B., F. D. Bello, J. H. C. Cornelissen, E. Laliberté, D. C. Laughlin, and P. B. Reich. 2016. Reinforcing loose foundation stones in trait-based plant ecology. Oecologia 180:923–931.

Shipley, B., C. E. T. Paine, and C. Baraloto. 2012. Quantifying the importance of local niche-based and stochastic processes to tropical tree community assembly. Ecology 93:760–769.

Siefert, A., C. Ravenscroft, M. D. Weiser, and N. G. Swenson. 2012. Functional beta- diversity patterns reveal deterministic community assembly processes in eastern North American trees. Global Ecology and Biogeography 22:682–691.

Siefert, A., C. Violle, L. Chalmandrier, C. H. Albert, A. Taudiere, A. Fajardo, L. W. Aarssen, et al. 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. (J. Chase, ed.)Ecology Letters 18:1406–1419.

Smith, A. B., B. Sandel, N. J. B. Kraft, and S. Carey. 2013. Characterizing scale-dependent community assembly using the functional-diversity–area relationship. Ecology 94:2392–2402.

Smith, T. W., and J. T. Lundholm. 2010. Variation partitioning as a tool to distinguish between niche and neutral processes. Ecography 33:648–655.

Soininen, J. 2014. A quantitative analysis of species sorting across organisms and ecosystems. Ecology 95:3284–3292.

———. 2016. Spatial structure in ecological communities – a quantitative analysis. Oikos 125:160–166.

Spasojevic, M. J., S. Copeland, and K. N. Suding. 2014. Using functional diversity patterns to explore metacommunity dynamics: a framework for understanding local and regional influences on community structure. Ecography 37:939–949.

Swenson, N. G. 2014. Functional and Phylogenetic Ecology in R. Springer Science & Business Media.

Swenson, N. G., P. Anglada-Cordero, and J. A. Barone. 2011. Deterministic tropical tree community turnover: evidence from patterns of functional beta diversity along an elevational gradient. Proceedings of the Royal Society B: Biological Sciences 278:877–884.

ter Braak, C. J. F. 2019. New robust weighted averaging- and model-based methods for assessing trait-environment relationships. Methods in Ecology and Evolution in press.

ter Braak, C. J. F., P. Šmilauer, and S. Dray. 2018. Algorithms and biplots for double constrained correspondence analysis. Environmental and Ecological Statistics 25:171–197.

Thompson, K., O. L. Petchey, A. P. Askew, N. P. Dunnett, A. P. Beckerman, and A. J. Willis. 2010. Little evidence for limiting similarity in a long-term study of a roadside plant community. Journal of Ecology 98:480–487.

Thompson, P. L., L. M. Guzman, L. De Meester, Z. Horváth, R. Ptacnik, B. Vanschoenwinkel, D. S. Viana, et al. 2020. A process-based metacommunity framework linking local and regional scale community ecology. Ecology Letters 23:1314–1329.

Tison-Rosebery, J., T. Leboucher, V. Archaimbault, J. Belliard, D. Carayon, M. Ferréol, M. Floury, et al. 2022. Decadal biodiversity trends in rivers reveal recent community rearrangements. Science of The Total Environment 823:153431.

Tucker, C. M., L. G. Shoemaker, K. F. Davies, D. R. Nemergut, and B. A. Melbourne. 2016. Differentiating between niche and neutral assembly in metacommunities using null models of β-diversity. Oikos 125:778–789.

Tuomisto, H., and K. Ruokolainen. 2006. Analyzing or explaining beta diversity? Understanding the targets of different methods of analysis. Ecology 87:2697–2708.

———. 2008. Analyzing or explaining beta diversity? reply. Ecology 89:3244–3256.

Viana, D. S., and J. M. Chase. 2019. Spatial scale modulates the inference of metacommunity assembly processes. Ecology 100:e02576.

Viana, D. S., P. Keil, and A. Jeliazkov. 2022. Disentangling spatial and environmental effects: Flexible methods for community ecology and macroecology. Ecosphere 13:e4028.

Villéger, S., G. Grenouillet, and S. Brosse. 2013. Decomposing functional β-diversity reveals that low functional β-diversity is driven by low functional turnover in European fish assemblages. Global Ecology and Biogeography 22:671–681.

Villéger, S., J. R. Miranda, D. F. Hernandez, and D. Mouillot. 2012. Low Functional β-Diversity Despite High Taxonomic β-Diversity among Tropical Estuarine Fish Communities. PLOS ONE 7:e40679.

Violle, C., B. J. Enquist, B. J. McGill, L. Jiang, C. H. Albert, C. Hulshof, V. Jung, et al. 2012. The return of the variance: intraspecific variability in community ecology. Trends in Ecology & Evolution 27:244–252.

Violle, C., M. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E. Garnier. 2007. Let the concept of trait be functional! Oikos 116:882–892.

Wang, X., N. G. Swenson, T. Wiegand, A. Wolf, R. Howe, F. Lin, J. Ye, et al. 2013. Phylogenetic and functional diversity area relationships in two temperate forests. Ecography 36:883–893.

Warton, D. I., B. Shipley, and T. Hastie. 2015. CATS regression – a model-based approach to studying trait-based community assembly. Methods in Ecology and Evolution 6:389–398.

Webb, C. T., J. A. Hoeting, G. M. Ames, M. I. Pyne, and N. L. Poff. 2010. A structured and dynamic framework to advance traits-based theory and prediction in ecology. Ecology Letters 13:267–283.

Weiher, E., G. D. P. Clarke, and P. A. Keddy. 1998. Community Assembly Rules, Morphological Dispersion, and the Coexistence of Plant Species. Oikos 81:309–322.

Weiher, E., D. Freund, T. Bunton, A. Stefanski, T. Lee, and Bentivenga Stephen. 2011. Advances, challenges and a developing synthesis of ecological community assembly theory. Philosophical Transactions of the Royal Society B: Biological Sciences 366:2403–2413.

Weiher, E., and P. A. Keddy. 1995. Assembly Rules, Null Models, and Trait Dispersion: New Questions from Old Patterns. Oikos 74:159–164.

Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs 30:279–338.

Whittaker, R. H. 2012. Classification of Plant Communities. Springer Science & Business Media.

Wood, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society: Series B (Statistical Methodology) 73:3–36.

Zelený, D. 2017. Bias in community-weighted mean analysis of plant functional traits and species indicator values. bioRxiv 046946.

———. 2018. Which results of the standard test for community-weighted mean approach are too optimistic? Journal of Vegetation Science 29:953–966.

References Cited Only in the Online Enhancements

Clappe, S., S. Dray, and P. R. Peres‐ Neto. 2018. Beyond neutrality: disentangling the effects of species sorting and spurious correlations in community analysis. Ecology 0.

Debastiani, V., and V. Pillar. 2012. SYNCSA – R tool for analysis of metacommunities based on functional traits and phylogeny of the community components. Bioinformatics 28:2067–2068.

Dray, S., P. Legendre, and P. R. Peres-Neto. 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecological Modelling 196:483–493.

Dray, S., R. Pélissier, P. Couteron, M.-J. Fortin, P. Legendre, P. R. Peres-Neto, E. Bellier, et al. 2012. Community ecology in the age of multivariate multiscale spatial analysis. Ecological Monographs 82:257–275.

Legendre, P., and E. D. Gallagher. 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129:271–280.

Legendre, P., D. Borcard, and P. R. Peres-Neto. 2005. Analyzing beta diversity: partitioning the spatial variation of community composition data. Ecological Monographs 75:435–450.

Legendre, P., D. Borcard, and P. R. Peres-Neto. 2008. Analyzing or explaining beta diversity? comment. Ecology 89:3238–3244.

Ovaskainen, O., D. B. Roy, R. Fox, and B. J. Anderson. 2016. Uncovering hidden spatial structure in species communities with spatially explicit joint species distribution models. Methods in Ecology and Evolution 7:428–436.

Petchey, O. L., A. Hector, and K. J. Gaston. 2004. How Do Different Measures of Functional Diversity Perform? Ecology 85:847–857.

Robroek, B. J. M., V. E. J. Jassey, R. J. Payne, M. Martí, L. Bragazza, A. Bleeker, A. Buttler, S. J. M. Caporn, N. B. Dise, J. Kattge, K. Zając, B. H. Svensson, J. van Ruijven, and J. T. A. Verhoeven. 2017. Taxonomic and functional turnover are decoupled in European peat bogs. Nature Communications 8.

Schloerke, B., J. Crowley, D. Cook, F. Briatte, M. Marbach, E. Thoen, A. Elberg, and J. Larmarange. 2018. GGally: Extension to “ggplot2.”

Vellend, M. 2010. Conceptual Synthesis in Community Ecology. The Quarterly Review of Biology 85:183–206.

Table 1

The nine exploratory categories used to classify the 1084 traits/trait modalities of the CESTES database (full data table in https://doi.org/10.57745/LLBAZD).

Code	Category	Description
Food	Food-related	Related to diet, food apprehension, nutrient assimilation and foraging techniques
Reproduction	Reproduction-related	Related to reproduction style or ability (e.g. number of eggs)
Mobility	Mobility-related	Related to mobility abilities, dispersal mode, propagule dissemination in space
Habitat	Habitat-related	Related to the association with habitat / substrate / physical milieu, specialization (e.g. host, microhabitat, etc.)
Body	Body-related	Related to morphological characteristics (e.g. size, wing length, florescence type, etc.) which can indeed be related to any function related to food extraction, reproduction, etc.
Tolerance	Tolerance to disturbance	Related to tolerance to any disturbance (fire regimes, drought, etc.)
Status	Status	Related to abundance, biogeographical distribution, rarity, threat level (e.g. harvesting pressure, red list level), patrimonial value, etc.
Life history	Life history	Related to life cycle characteristics, phenology and ecological strategies
Others	Others	Traits that could not at all be classified or that mix / integrate different types of information (including customized traits): e.g. species thermal index, home range size, competitive strategy, symbiont, vertical stratification, survival, behavioral innovation rate, fluorescence, productivity, taxonomic family, burrowing ability, number of hosts exploited.

Figure legends

Figure 1. Conceptual illustration of the two main analyses performed in this synthesis adapted from Swenson et al. 2011; de Bello et al. 2013; Escobedo et al. 2021. In a), the processes written in italics are interpretations that are less widely-shared in the field of community ecology or have received less attention in terms of theoretical or empirical justification.

Figure 2. Trait-related determinism in metacommunity structure. Plot of the Standardized Effect Size (SES) of the total functional beta diversity for each a) dataset and b) study group, showing in which cases the multi-trait (big dots) and single-trait (small dots) functional turnover is lower (blue) or higher (red) than expected given the taxonomic turnover—interpreted as potential metacommunity processes of functional convergence due to habitat selection, or functional divergence due to limiting similarity (competition), respectively. Distribution of the proportion of structuring traits (i.e. that allowed detecting significant trait dispersion) across c) biological kingdoms, and d) ecosystem types / realms.

Figure 3. Structuring and non-structuring traits. a) Overall percentage of traits / trait modalities (1084 modalities) in each trait category (see **Table 1**) across the 80 datasets; b) Proportion of traits showing significant dispersion across space in each trait category.

Figure 4. Relative sensitivity of the pairwise Functional Beta Diversity to environment. a) Variation of pairwise functional (FBDp) and taxonomic (TBDp) beta diversity explained by the environmental variation for every dataset compared to the 1:1 line (dotted line); b) Sensitivity of functional beta diversity to environment relative to taxonomic beta diversity sensitivity measured as the difference of variation explained by environment between functional beta diversity (R^2_{FBDp}) and taxonomic beta diversity (R^2_{TBDp}).

Figure 5. Synthesis of the relative sensitivity of pairwise Functional Beta Diversity to environment. Results from the meta-analysis model examining the relationship between the relative sensitivity of FBDp to environment and different a) ecological features – level of disturbance, dispersal mode, spatial extent – and sampling properties – number of sites, number of environmental predictors (Nb Env), and traits-species trade-off (Nb Traits vs. Nb Species) – of the datasets, and b) their interactions. Dots are the posterior medians, the black thick whiskers are the 50% confidence intervals and the thin grey whiskers are the 95% confidence interval (BRMS outputs: **Appendix S12**; additional plots: **Appendix S11**).

Figure 1

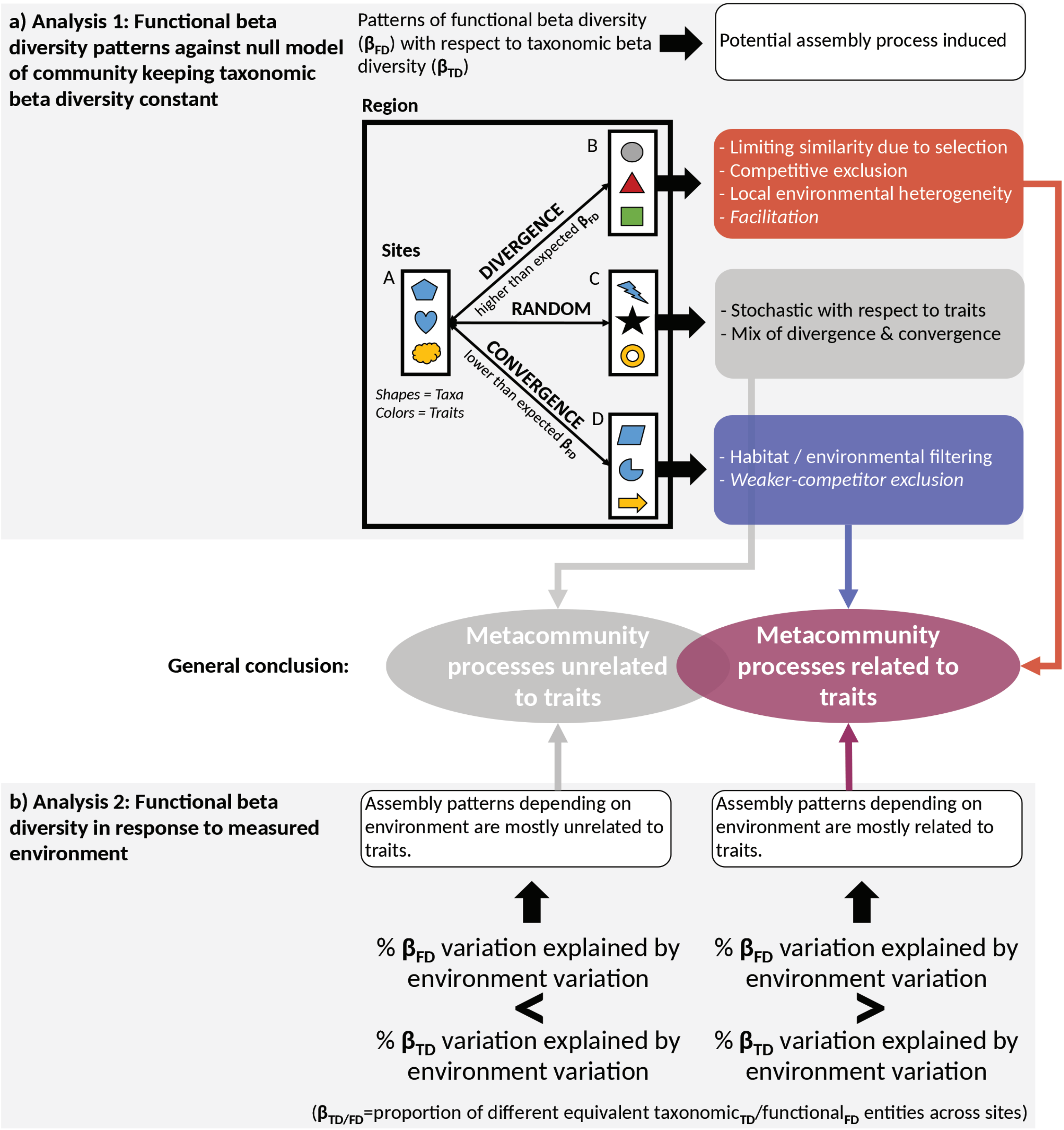

a) Analysis 1: Functional beta diversity patterns against null model of community keeping taxonomic beta diversity constant
Patterns of functional beta diversity (β_{FD}) with respect to taxonomic beta diversity (β_{TD})
Potential assembly process induced
Region
B
Sites
A
C
D
DIVERGENCE
higher than expected β_{FD}
RANDOM
CONVERGENCE
lower than expected β_{FD}
Shapes = Taxa
Colors = Traits
- Limiting similarity due to selection
- Competitive exclusion
- Local environmental heterogeneity
- Facilitation
- Stochastic with respect to traits
- Mix of divergence & convergence
- Habitat / environmental filtering
- Weaker-competitor exclusion
General conclusion:
Metacommunity processes unrelated to traits
Metacommunity processes related to traits
b) Analysis 2: Functional beta diversity in response to measured environment
Assembly patterns depending on environment are mostly unrelated to traits.
Assembly patterns depending on environment are mostly related to traits.
% β_{FD} variation explained by environment variation
<
% β_{TD} variation explained by environment variation
% β_{FD} variation explained by environment variation
>
% β_{TD} variation explained by environment variation
($\beta_{TD/FD}$=proportion of different equivalent taxonomic$_{TD}$/functional$_{FD}$ entities across sites)

Figure 2

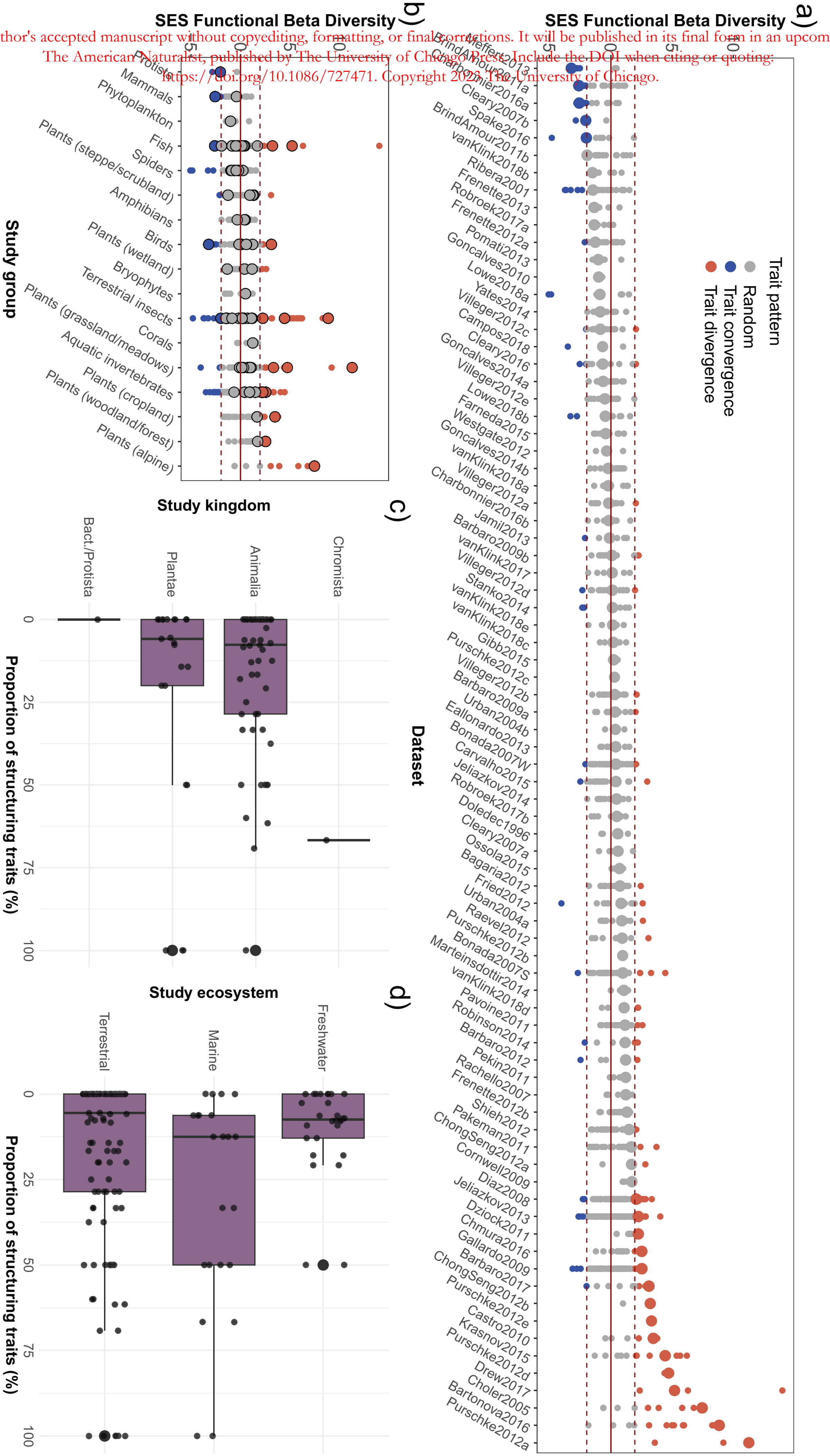

a)
SES Functional Beta Diversity
-5
0
5
10
Dataset
Trait pattern
● Random
● Trait convergence
● Trait divergence
Helfrtz2013
BrindAmour2011a
Charbonnier2016a
Cleary2007b
Spake2016
BrindAmour2011b
vanKlink2018b
Ribera2001
Frenette2013
Robroek2017a
Frenette2012a
Pomati2013
Goncalves2010
Lowe2018a
Yates2014
Villeger2012c
Campos2018
Cleary2016
Goncalves2014a
Villeger2012e
Lowe2018b
Farneda2015
Westgate2012
Goncalves2014b
vanKlink2018a
Villeger2012a
Charbonnier2016b
Jamil2013
Barbaro2009b
vanKlink2017
Villeger2012d
Stanko2014
vanKlink2018e
vanKlink2018c
Gibb2015
Purschke2012c
Villeger2012b
Barbaro2009a
Urban2004b
Eallonardo2013
Bonada2007W
Carvalho2015
Jeliazkov2014
Robroek2017b
Doledec1996
Cleary2007a
Ossola2015
Bagaria2012
Fried2012
Urban2004a
Raevel2012
Purschke2012b
Bonada2007S
Marteinsdottir2014
vanKlink2018d
Pavoine2011
Robinson2014
Barbaro2012
Pekin2011
Rachello2007
Frenette2012b
Shieh2012
Pakeman2011
ChongSeng2012a
Cornwell2009
Diaz2008
Jeliazkov2013
Dziock2011
Chmura2016
Gallardo2009
Barbaro2017
ChongSeng2012b
Purschke2012e
Castro2010
Krasnov2015
Purschke2012d
Drew2017
Choler2005
Bartonova2016
Purschke2012a
b)
SES Functional Beta Diversity
-5
0
5
10
Study group
Protists
Mammals
Phytoplankton
Fish
Spiders
Plants (steppe/scrubland)
Amphibians
Birds
Plants (wetland)
Bryophytes
Terrestrial insects
Corals
Plants (grassland/meadows)
Aquatic invertebrates
Plants (cropland)
Plants (woodland/forest)
Plants (alpine)
c)
Study kingdom
Bact./Protista
Plantae
Animalia
Chromista
0
25
50
75
100
Proportion of structuring traits (%)
d)
Study ecosystem
Terrestrial
Marine
Freshwater
0
25
50
75
100
Proportion of structuring traits (%)

Figure 3

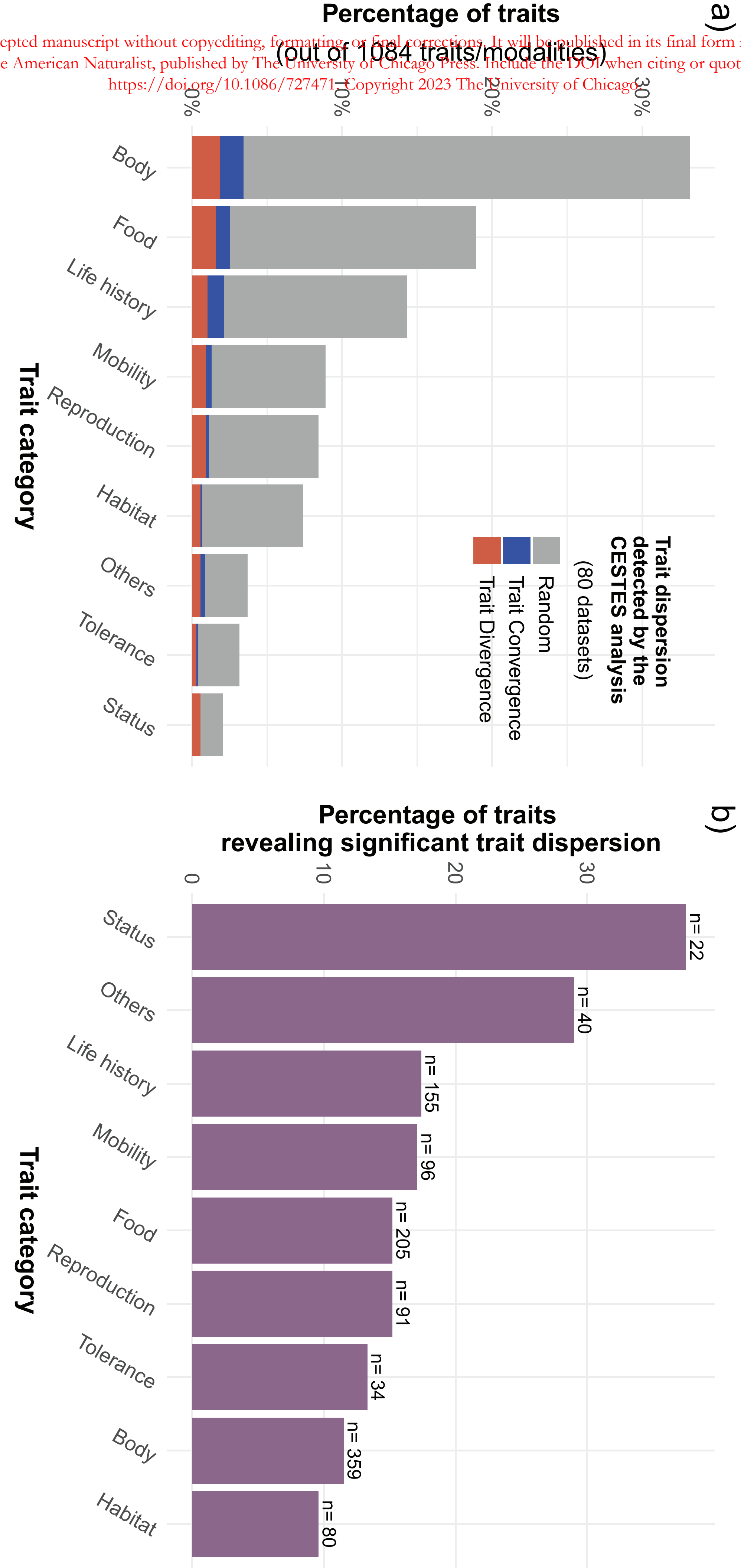

a)
Percentage of traits
(out of 1084 traits/modalities)
0%
10%
20%
30%
Trait category
Body
Food
Life history
Mobility
Reproduction
Habitat
Others
Tolerance
Status
Trait dispersion
detected by the
CESTES analysis
(80 datasets)
Random
Trait Convergence
Trait Divergence
b)
Percentage of traits
revealing significant trait dispersion
0
10
20
30
Trait category
Status
Others
Life history
Mobility
Food
Reproduction
Tolerance
Body
Habitat
n= 22
n= 40
n= 155
n= 96
n= 205
n= 91
n= 34
n= 359
n= 80

Figure 4

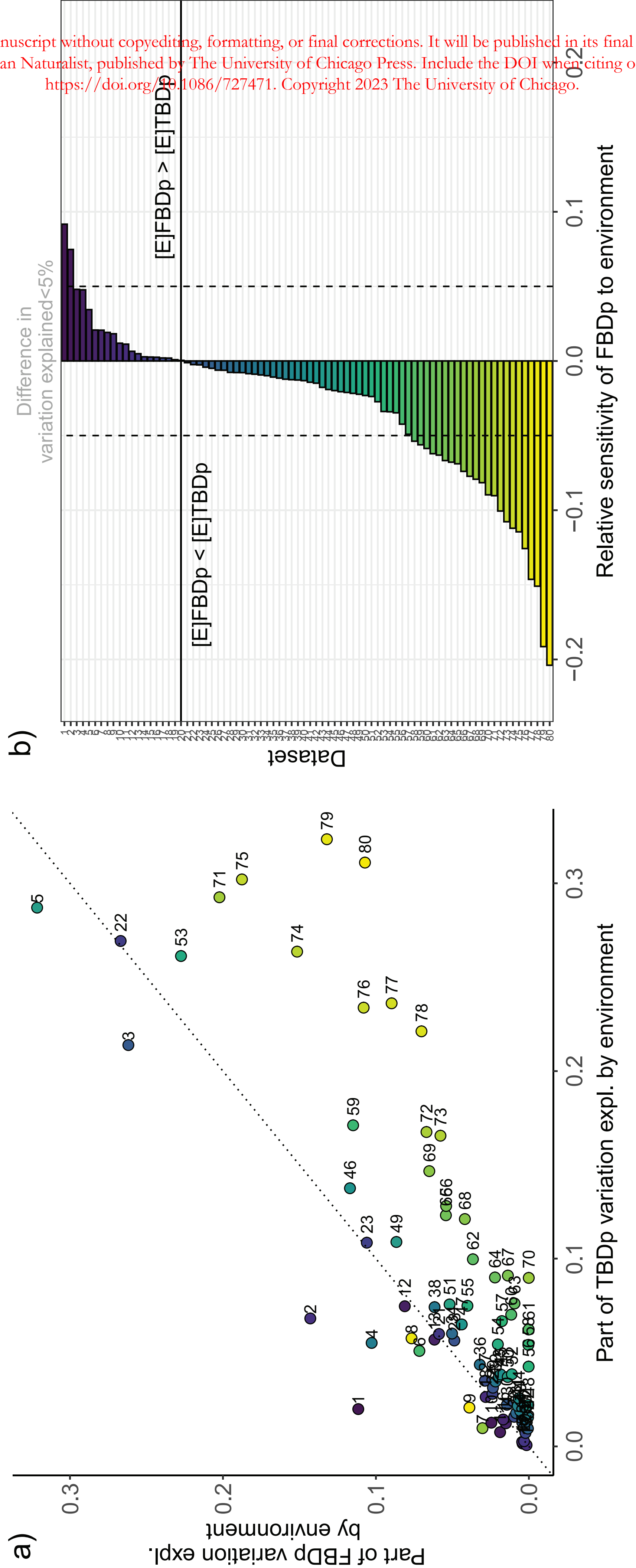
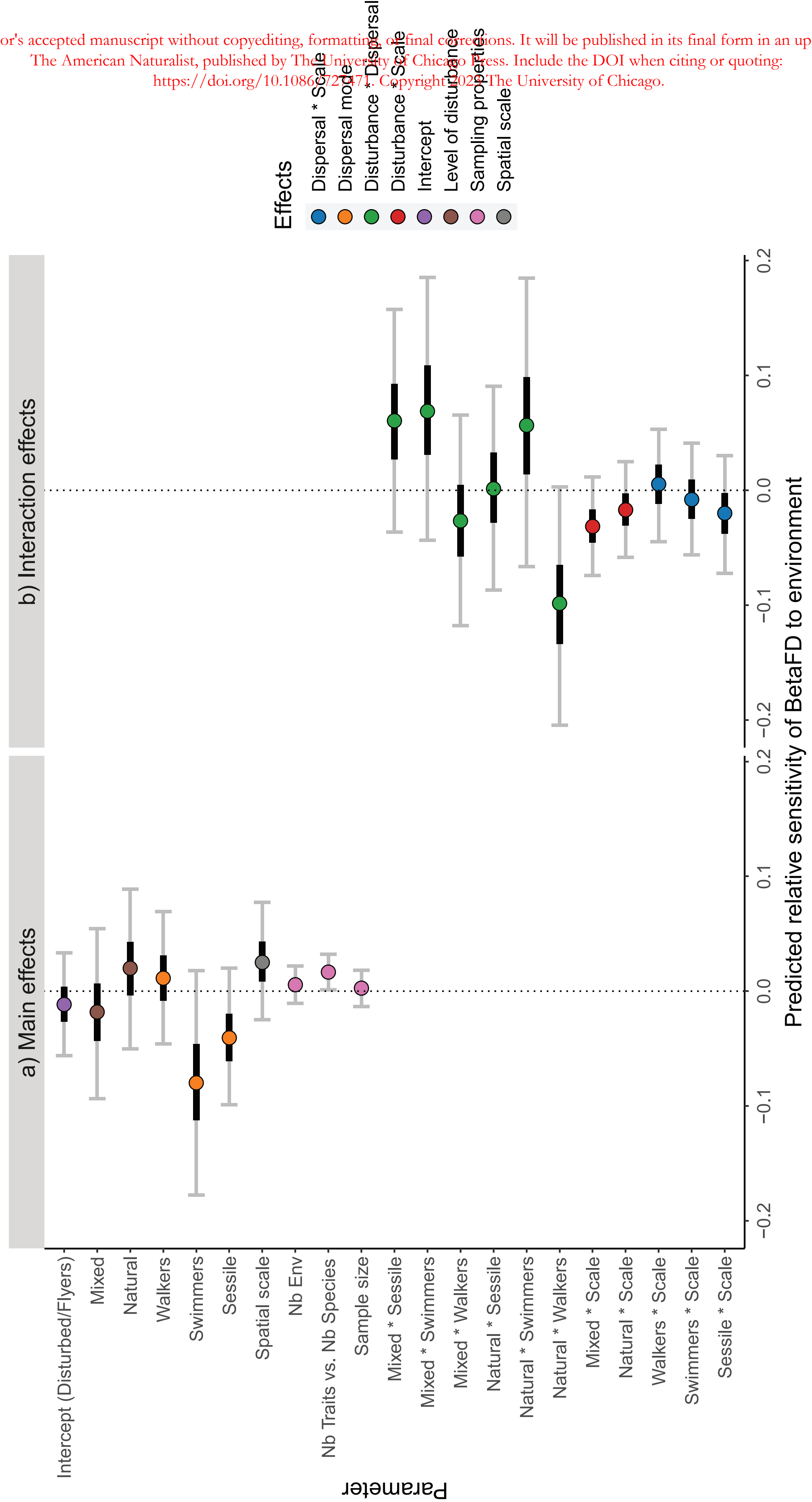

a)
Part of FBDp variation expl. by environment
0.0
0.1
0.2
0.3
Part of TBDp variation expl. by environment
b)
Dataset
Relative sensitivity of FBDp to environment
−0.2
−0.1
0.0
0.1
0.2
Difference in variation explained<5%
[E]FBDp > [E]TBDp
[E]FBDp < [E]TBDp
1
2
3
4
5
22
23
46
49
53
59
71
74
75
76
77
78
79
80

Figure 5


a) Main effects
b) Interaction effects
Effects
Dispersal * Scale
Dispersal mode
Disturbance * Dispersal
Disturbance * Scale
Intercept
Level of disturbance
Sampling properties
Spatial scale
Parameter
Intercept (Disturbed/Flyers)
Mixed
Natural
Walkers
Swimmers
Sessile
Spatial scale
Nb Env
Nb Traits vs. Nb Species
Sample size
Mixed * Sessile
Mixed * Swimmers
Mixed * Walkers
Natural * Sessile
Natural * Swimmers
Natural * Walkers
Mixed * Scale
Natural * Scale
Walkers * Scale
Swimmers * Scale
Sessile * Scale
−0.2
−0.1
0.0
0.1
0.2
Predicted relative sensitivity of BetaFD to environment

Supporting Information

When do traits tell more than species about a metacommunity? A synthesis across ecosystems and scales

Authors

Alienor Jeliazkov[1] & Jonathan M. Chase[2,3]

Affiliations

[1]University of Paris-Saclay, INRAE, HYCAR, 1 rue Pierre Gilles de Gennes, 92160 Antony, France

[2]German Centre for Integrative Biodiversity Research (iDiv), Deutscher Platz 5E, 04103 Leipzig, Germany

[3]Department of Computer Science, Martin Luther University Halle-Wittenberg, 06099 Halle (Salle), Germany

Corresponding author: Alienor Jeliazkov: alienor.jeliazkov@gmail.com; alienor.jeliazkov@inrae.fr

Journal: The American Naturalist

Appendix S1. Overview of the CESTES database

The CESTES database comes from the following data paper:

Jeliazkov, A. et al. 2020. A global database for metacommunity ecology, integrating species, traits, environment and space. - Scientific Data 7: 1–15.

This database assembles 80 datasets from studies that analyzed empirical multivariate trait-environment relationships between 1996 and 2018. Each of these datasets include four data matrices: community data (species abundances or presences/absences across multiple sites), species traits (*sensu lato*), environmental variables across sites, and spatial coordinates. The database is global in extent and covers different taxonomic groups, ecosystem types, levels of human disturbance, and spatial scales (Jeliazkov et al. 2020: Fig.2).

The main condition for dataset eligibility was that trait-environment relationships were the focus of the study and data use. This ensured that: (i) the trait and the taxonomic information were collected from similar biogeographic areas (minimizing mismatches between the geographic origins of trait and taxonomic data), (ii) the sampled sites were associated with background environmental information that was relevant to the community and traits under study. Jeliazkov et al. (2020) focused on studies that included “RLQ” and “fourth-corner” terms because both of them are prevailing methods of multivariate trait-based analyses in ecology. This focus ensures that most of the datasets (i) are multivariate and include both several species, several traits, and several sites (spatial information) to align with a metacommunity-like structure, (ii) have a comparable structure and can be used in comparative analyses and syntheses. To know more about the data search and collection methodology, see Jeliazkov et al. 2020.

The datasets are summarized in the **Table S1.1** below (for more information, see Jeliazkov et al. 2020) and are available at:

https://idata.idiv.de/ddm/Data/ShowData/286

https://doi.org/10.6084/m9.figshare.c.4459637.v1

https://doi.org/10.57745/LLBAZD (additional data formats + all of the R scripts used for data processing and analyses).

Table S1.1. Table with the metadata (extracted from Jeliazkov et al. 2020) and the study identifier used in our mixed model (see main text). nbEnv, nbTra, nbSpe and nbSit are the numbers of environmental variables, traits, species and sites, respectively.

DatasetName	Ecosystem and location	Study id	Taxonomic group	Ecosystem type	Extent (km2)	Type of disturbance	Sampling date(s)/period	nbEnv	nbTra	nbSpe	nbSit
Bagaria2012	Mediterranean semi-natural mountain grasslands, southern Catalonia, Spain	1	Plants	Terrestrial	2000	Semi-natural	2007	8	13	49	29
Barbaro2009a	Intensive pine plantations, mosaic forest landscapes in south-western France	2	Beetles	Terrestrial	32.16	Forestry	2002-2003	11	12	36	195
Barbaro2009b	Intensive pine plantations, mosaic forest landscapes in south-western France	2	Birds	Terrestrial	32.16	Forestry	2002-2003	11	12	53	201
Barbaro2012	Fragmented native forests, volcanic banks peninsula, Canterbury, South Island, New Zealand	3	Birds	Terrestrial	625	Natural	2010–2011	6	7	21	26
Barbaro2017	Vineyards, Aquitaine, France	4	Birds	Terrestrial	750	Agricultural	2013	6	8	56	20
Bartonova2016	National Nature Reserves and National Natural Monuments, Czech Republic	5	Butterflies	Terrestrial	78866	Natural	2004 – 2006	11	13	128	122
Bonada2007S	Mediterranean rivers, Catalonia, Spain	6	Macroinvertebrates	Freshwater	96.3	Natural	summer 1996	16	63	70	17
Bonada2007W	Mediterranean rivers, Catalonia, Spain	6	Macroinvertebrates	Freshwater	96.3	Natural	winter 1996	14	63	44	22
BrindAmour2011a	Drouin lake, Laurentian Shield Lakes, Quebec, Canada	7	Fishes	Freshwater	0.31	Semi-natural	2001	19	24	7	90
BrindAmour2011b	Pare lake, Laurentian Shield Lakes, Quebec, Canada	7	Fishes	Freshwater	0.23	Semi-natural	2001	17	24	6	60
Campos2018	Tropical floodplain lakes, Upper Paraná River floodplain, Brazil	8	Ostracods	Freshwater	700	Mixed	2011	7	2	37	27
Carvalho2015	Tocantins-Araguaia river basin, Amazonia, Brazil	9	Stream fishes	Freshwater	180000	Mixed	2008	8	26	65	27
Castro2010	Southern Portugal	10	Plants	Terrestrial	1.9844	Agricultural	NA	8	6	28	9
Charbonnier2016a	Forests, Europe	11	Bats	Terrestrial	4400000	Forestry	2012-2013	5	9	27	175
Charbonnier2016b	Forests, Europe	11	Birds	Terrestrial	4400000	Forestry	2012-2013	5	10	73	208
Chmura2016	Karkonosze Mts, Sudeten Mts, Poland	12	Plants	Terrestrial	135.05	Natural	NA	10	17	46	364
ChongSeng2012a	Seychelles archipelago	13	Coral reef fishes	Marine	3600	Semi-natural	2010	17	2	147	79
ChongSeng2012b	Seychelles archipelago	13	Coral reef fishes	Marine	3600	Semi-natural	2012	12	2	155	78
Cleary2007a	Mentaya river, Central Kalimantan province, Borneo, Indonesia	14	Birds	Terrestrial	196	Mixed	1997-1998	36	4	145	37
Cleary2007b	Coral reefs, Spermonde Archipelago, Makassar, southwest Sulawesi, Indonesia	15	Foraminifera	Marine	2418	Mixed	1997	10	3	24	31

Cleary2016	Coral reefs, Jakarta, Indonesia	16	Fishes	Marine	1764	Fishing	2005	21	15	162	27
Cornwell2009	Jasper Ridge Biological Preserve, Coastal, California, USA	17	Woody plants	Terrestrial	4.81	Semi-natural	2002-2003	3	3	42	34
Diaz2008	Segura River basin,SE Spain	18	Macroinvertebrates	Freshwater	6300	Mixed	1999-2001	39	62	208	104
Doledec1996	Urban-rural gradient, Lyon, France	19	Birds	Terrestrial	96	Mixed	1981	11	4	40	51
Drew2017	Archipelagos, Melanesia	20	Coral reef fishes	Marine	15300000	Mixed	NA	1	3	188	7
Dziock2011	Dessau, Magdeburg, Elbe, Floodplain, Sachsen-Anhalt, Germany	21	Grasshopers	Terrestrial	224	Agricultural	2006	5	6	16	34
Farneda2015	Biological Dynamics of Forest Fragments Project (BDFFP) located ca. 80 km north of Manaus, Central Amazon, Brazil	22	Bats	Terrestrial	680	Natural	2011-2013	9	8	41	17
Frenette2012a	Arid steppes, Eastern Morocco	23	Plants	Terrestrial	11765	Mixed	2009	5	18	32	50
Frenette2012b	Arid steppes, Eastern Morocco	23	Plants	Terrestrial	11765	Mixed	2010	5	18	32	50
Frenette2013	Arid steppes, Eastern Morocco	23	Ants	Terrestrial	11765	Mixed	2010	5	6	22	22
Fried2012	Agriculture areas, France	24	Plants	Terrestrial	386000	Agricultural	2003-2006	11	10	75	218
Gallardo2009	Ebro river, Mediterranee, Spain	25	Macroinvertebrates	Freshwater	11	Agricultural	2006	30	87	35	76
Gibb2015	Themeda grasslands, south-east Australia	26	Spiders	Terrestrial	37.64970119	Mixed	2009-2011	7	10	86	36
Goncalves2010	Santa Lucia Biological Station (SLBS), Santa Teresa County, Espirito Santo State, southeast Brazil	27	Spiders	Terrestrial	0.44	Natural	2006-2007	1	4	146	45
Goncalves2014a	Open restingas, Atlantic rainforest, Brazil	28	Spiders	Terrestrial	220000	Natural	2009	10	22	105	309
Goncalves2014b	Open restingas, Atlantic rainforest, Brazil	28	Spiders	Terrestrial	220000	Natural	2010	10	22	112	356
Jamil2013	Terschelling island, dune meadow, Netherlands	29	Plants	Terrestrial	84	Agricultural	1982	5	5	28	20
Jeliazkov2013	Ponds, agricultural areas, Brie, Seine-et-Marne, France	30	Macroinvertebrates	Freshwater	430	Agricultural	2012	47	91	112	200
Jeliazkov2014	Ponds, agricultural areas, Brie, Seine-et-Marne, France	30	Amphibians	Freshwater	430	Agricultural	2011-2012	9	16	11	135
Krasnov2015	Palearctic area; Slovakia	31	Flea	Terrestrial	33000000	Mixed	1958, 2008	17	13	177	45
Lowe2018a	Urban gradient, Sydney, Australia	32	Spiders	Terrestrial	1000	Mixed	2013	33	7	135	115
Lowe2018b	Urban gradient, focus on gardens, Sydney, Australia	32	Spiders	Terrestrial	1000	Mixed	2013	20	7	95	65
Marteinsdottir2014	Grazed ex-arable fields and semi-natural grasslands, southeast Sweden	33	Plants	Terrestrial	12	Mixed	2007-2008	7	3	39	14
Meffert2013	Urban wasteland, Berlin, Germany	34	Birds	Terrestrial	892	Urban	2007	4	5	30	54
Ossola2015	Urban habitat, south-eastern Melbourne, Australia	35	Ants	Terrestrial	100	Urban	2013-2014	20	5	60	29
Pakeman2011	Drumbuie, Scotland	36	Plants	Terrestrial	35	Agricultural	2007	33	28	148	30
Pavoine2011	Coastal marsh plain Mekhada in the east of Annaba , La Mafragh, Algeria	37	Plants	Terrestrial	100	Agricultural	1979	8	14	56	97

Pekin2011	Walpole and Albany, SW Australia	38	Plants	Terrestrial	1073	Semi-natural	2007	17	4	183	16
Pomati2013	peri-alpine mesotrophic Lake Zürich, Switzerland	39	Phytoplankton	Freshwater	88.66	Mixed	2009	8	15	20	15
Purschke2012a	Semi-natural grasslands, Jordtorp area, Öland Baltic Island, Sweden	40	Plants	Terrestrial	20.25	Semi-natural	2007	12	2	164	113
Purschke2012b	Semi-natural grasslands, Jordtorp area, Öland Baltic Island, Sweden	40	Plants	Terrestrial	20.25	Semi-natural	2007	12	1	53	113
Purschke2012c	Semi-natural grasslands, Jordtorp area, Öland Baltic Island, Sweden	40	Plants	Terrestrial	20.25	Semi-natural	2007	12	1	145	113
Purschke2012d	Semi-natural grasslands, Jordtorp area, Öland Baltic Island, Sweden	40	Plants	Terrestrial	20.25	Semi-natural	2007	12	1	117	113
Purschke2012e	Semi-natural grasslands, Jordtorp area, Öland Baltic Island, Sweden	40	Plants	Terrestrial	20.25	Semi-natural	2007	12	1	137	113
Rachello2007	Coral reefs, Jakarta, Indonesia	41	Corals	Marine	2242	Mixed	1995	47	5	93	27
Raevel2012	Montpellier district, Mediterranean vertical outcrops	42	Plants	Terrestrial	1886	Semi-natural	2008-2009	3	7	97	52
Ribera2001	Scotland	43	Beetles	Terrestrial	78772	Mixed	1995-1997	19	20	68	87
Robinson2014	Various habitats, protected reserves, Prague region, Czech Republic	44	Butterflies	Terrestrial	260	Semi-natural	2003-2004	7	6	71	20
Robroek2017a	Peat bogs, Western Europe	45	Vascular plants	Terrestrial	3800000	Natural	2010-2011	9	5	15	56
Robroek2017b	Peat bogs, Western Europe	45	Bryophytes	Terrestrial	3800000	Natural	2010-2011	9	12	10	56
Shieh2012	Wu Stream, central Taiwan	46	Macroinvertebrates	Freshwater	696	Mixed	2005-2006	11	38	30	48
Spake2016	Coniferous plantations, UK	47	Beetles	Terrestrial	95000	Forestry	1995-1997	9	6	51	44
Stanko2014	Slovakia	48	Flea	Terrestrial	12000	Agricultural	1986, 1990	16	6	27	13
Urban2004a	Ponds, 200-ha section of the Yale-Myers Research Station in Union, Connecticut, USA	49	Macroinvertebrates	Freshwater	2	Mixed	1999-2000	6	14	71	14
Urban2004b	Ponds, 200-ha section of the Yale-Myers Research Station in Union, Connecticut, USA	49	Amphibians	Freshwater	2	Mixed	1999-2000	6	2	7	11
vanKlink2017	Low intensity hay meadows, Swiss Plateau, Switzerland	50	Plants	Terrestrial	12154	Agricultural	2014-2015	11	5	129	35
vanKlink2018a	Low intensity hay meadows, Swiss Plateau, Switzerland	50	Bees	Terrestrial	12154	Agricultural	2014-2015	11	7	46	35
vanKlink2018b	Low intensity hay meadows, Swiss Plateau, Switzerland	50	Moths	Terrestrial	12154	Agricultural	2014-2015	11	7	87	35
vanKlink2018c	Low intensity hay meadows, Swiss Plateau, Switzerland	50	Ground beetles	Terrestrial	12154	Agricultural	2014-2015	11	7	60	33
vanKlink2018d	Low intensity hay meadows, Swiss Plateau, Switzerland	50	Rove beetles	Terrestrial	12154	Agricultural	2014-2015	11	4	82	32
vanKlink2018e	Low intensity hay meadows, Swiss Plateau, Switzerland	50	Hoverflies	Terrestrial	12154	Agricultural	2014-2015	11	6	26	35

Villeger2012a	Estuarine ecosystem,Terminos Lagoon, Gulf of Mexico, Mexico	51	Fish	Marine	3360	Semi-natural	May-03	4	16	45	35
Villeger2012b	Estuarine ecosystem,Terminos Lagoon, Gulf of Mexico, Mexico	51	Fish	Marine	3360	Semi-natural	Jul-03	4	16	48	34
Villeger2012c	Estuarine ecosystem,Terminos Lagoon, Gulf of Mexico, Mexico	51	Fish	Marine	3360	Semi-natural	Nov-03	4	16	47	34
Villeger2012d	Estuarine ecosystem,Terminos Lagoon, Gulf of Mexico, Mexico	51	Fish	Marine	3360	Semi-natural	May-06	4	16	43	35
Villeger2012e	Estuarine ecosystem,Terminos Lagoon, Gulf of Mexico, Mexico	51	Fish	Marine	3360	Semi-natural	Jul-06	4	16	46	35
Westgate2012	Eucalypt forest, Booderee National Park, Australia	52	Amphibians	Terrestrial	98	Natural	2007-2008	6	2	12	43
Yates2014	Pasture vs remnant vegetation, North east of New South Wales, Australia	53	Ants	Terrestrial	45500	Mixed	2007	9	11	123	18
Eallonardo2013	Inland salt/marsh, New York State, USA, near Montezuma; Carncross, Howland Island and Fox Ridge	54	Plants	Mixed	3.5	Natural	2007	14	14	41	76
Choler2005	Southwestern Alps, Aravo, Grand Galibier, France	55	Plants	Terrestrial	0.02	Semi-natural	2001	7	8	82	75

Appendix S2. Calculation of taxonomic and functional beta diversity

a) Total Taxonomic and Functional Beta Diversities ("TBD" and "FBD")

The normalized proportional beta-equivalent-additive index proposed by de Bello et al. (2010) ("beta_prop") "represents the proportion of diversity accounted for by the differentiation between communities (or sampling units) in a given region" and "can be expressed as a percentage of the diversity of a whole region" by standardizing it by the regional diversity (gamma). The final calculation of this beta index can be expressed as follows:

$$\beta_{Norm-prop} = \frac{n}{n-1} \times \left(1 - \frac{1-\gamma_{Rao}}{1-\alpha_{Rao}}\right)$$

where n is the number of sampling units, α_{Rao} the mean local Rao diversity (the expected dissimilarity between two randomly chosen individuals from a sampled community), and γ_{Rao} the regional Rao diversity (the expected dissimilarity between two randomly chosen individuals from the whole metacommunity), with:

$$\alpha_{Rao} = \sum_{i=1}^{s}\sum_{j=1}^{s} d_{ij} p_{ic} p_{jc}$$

where d_{ij} is the dissimilarity/distance measure between species i and species j from the local community of s species, and p_{ic}, and p_{jc} the proportion of the species i, and j in the community, respectively (based on their relative abundances). d_{ij} can be any type of dissimilarities/distances (taxonomic, functional, phylogenetic, etc.) depending on the biodiversity facet investigated and scales between 0 and 1. In the case of the taxonomic distances, $d_{ij} = 1$ for every $i \neq j$ and α_{Rao} equates the Simpson index. For the functional version of the index, we calculated the functional distances between species as Gower distances (Podani 1999) on raw traits (function 'gowdis' in package {FD}) including appropriate weighting for dummy traits (e.g. several levels for a given categorical traits) in order to get equal contribution of the different traits.

Similarly, the regional diversity index γ_{Rao} is expressed as:

$$\gamma_{Rao} = \sum_{i=1}^{S}\sum_{j=1}^{S} d_{ij} P_i P_j$$

where d_{ij} is the dissimilarity measure between species i and species j from the whole metacommunity of S species, and P_i, and P_j the proportion of the species i, and j in the metacommunity, respectively. To see the full development of the $\beta_{Norm-prop}$ equation, see de Bello et al. (2010).

TBD, and FBD correspond to the taxonomic, and functional $\beta_{Norm-prop}$, respectively.

This $\beta_{Norm-prop}$ index can be interpreted as the proportion of different equivalent species/functional entities found across all sampling units (α_{Rao}) with respect to the total regional diversity (γ_{Rao}), which is useful when comparing different facets of diversity (e.g. taxonomic, functional, phylogenetic) (de Bello et al. 2010).

b) Pairwise Taxonomic and Functional Beta Diversities (“TBDp” and “FBDp”)

The pairwise version of the $\beta_{Norm-prop}$ index consists in calculating this same index for each pair of sites. Each pairwise beta can thus be expressed as:

$$\beta_{ab} = \frac{\gamma_{ab} - (\alpha_a + \alpha_b)/2}{\gamma_{ab}}$$

where γ_{ab} is the number of equivalent species/functional entities over the pair of sites a and b, α_a is the number of equivalent species/functional entities of the site a and α_b is the number of equivalent species/functional entities of the site b (see de Bello et al. 2010).

TBDp, and FBDp correspond to the entire sites-by-sites matrices of taxonomic, and functional pairwise β_{ab}s, respectively.

This β_{ab} index can be interpreted as the proportion of different equivalent species/functional entities found across two sampling units (α_a,α_b) with respect to the total diversity of the pair of sites (γ_{ab}). As such, it reflects the pairwise dissimilarity across sites in terms of assemblage differences. Thus, pairs of sites that have higher β_{ab} tend to have more different assemblages than pairs of sites that have lower β_{ab}.

c) Note

It is important to note that the interpretation of the $\beta_{Norm-prop}$ index strongly depends on what is considered as the regional species pool (de Bello 2012). In our case, we considered the full community, as it was done in the original studies from which we collected the data. The region indeed is a unit that is difficult to delineate, with sometimes a quite subjective scale. However, in all of the 80 original case studies, the whole pool was considered to study the ecology of the focused community and no region stratification was applied. Therefore, we considered the full community as the regional pool for the null modeling procedure.

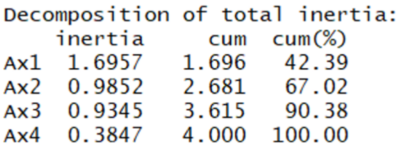
References

de Bello, F. 2012. The quest for trait convergence and divergence in community assembly: are null-models the magic wand? - Global Ecology and Biogeography 21: 312–317.

de Bello, F. et al. 2010. The partitioning of diversity: showing Theseus a way out of the labyrinth. - Journal of Vegetation Science 21: 992–1000.

Appendix S3. Summary of the sampling properties

The sampling properties were derived from a Principal Component Analysis performed on the four variables: number of sites, number of environmental variables, number of species, and number of traits for each dataset. This PCA thus allowed us to reduce the sampling properties information (that was partly correlated) into three main orthogonal axes (that explained altogether 90% of the variation, **Fig. S3.1**).



```
Decomposition of total inertia:
    inertia      cum   cum(%)
Ax1  1.6957    1.696    42.39
Ax2  0.9852    2.681    67.02
Ax3  0.9345    3.615    90.38
Ax4  0.3847    4.000   100.00
```

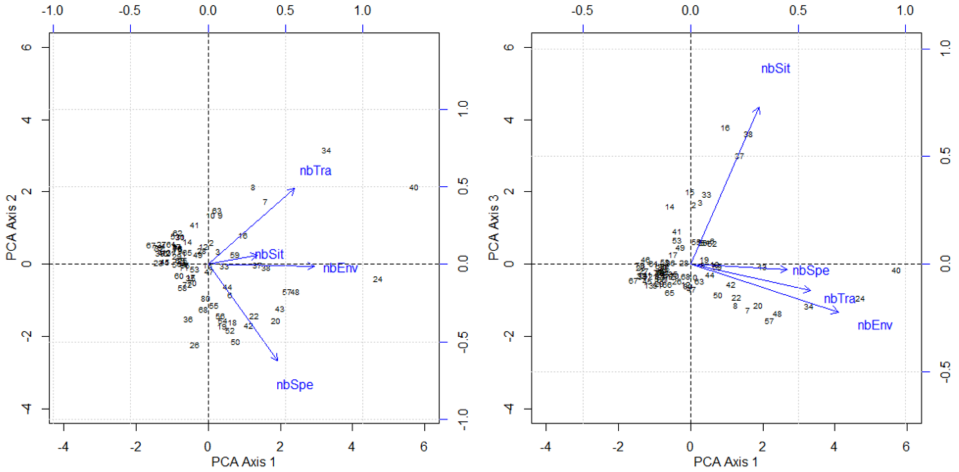


Figure S3.1. Results from the Principal Component Analysis applied on the four sampling properties, namely the sample size (“nbSit”), number of environmental variables (“nbEnv”), number of species (“nbSpe”), and number of traits (“nbTra”). The 1st PCA axis explains 42% of the variability and is mainly driven by the number of environmental variables. The 2nd axis explains an additional 25% of the variability and is mainly driven by the increase of the number of traits at the expense of the number of species. The 3rd axis explains an additional 23% of the variability and is mainly driven by the increase of sample size. The coordinates of the studies along these three axes constituted the synthetic variables of sampling properties used in the final synthesis model, namely the “Nb Env” (the number of environmental variables, the “Nb Traits vs. Nb of species” trade-off, and the “Sample size”, respectively.

Appendix S4. Data exploration

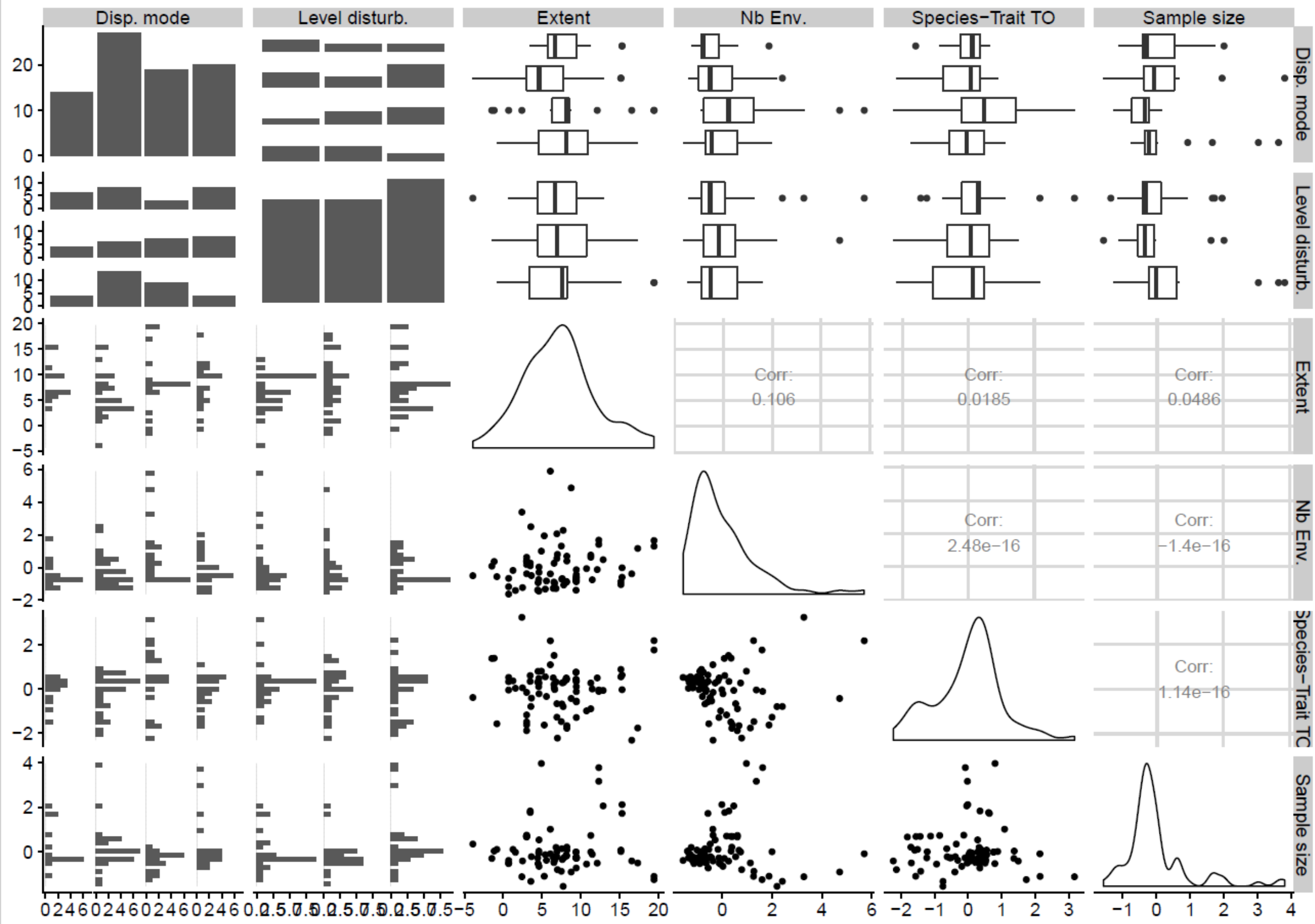
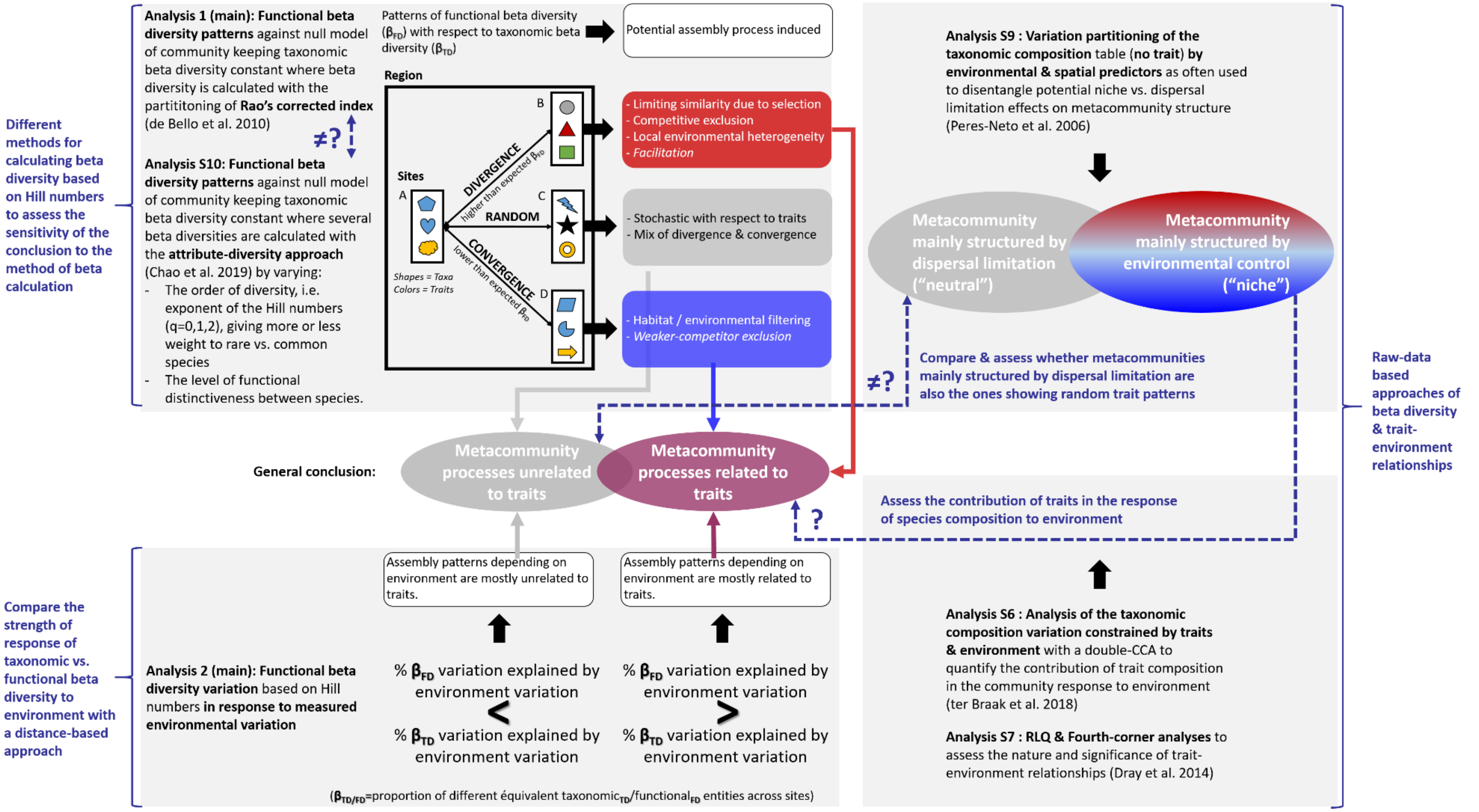


Figure S4.1. Generalized pair plots for the three ecological features and three sampling properties used as predictors in the synthesis model. On the diagonal: distribution of the variable values. On the upper triangle panel: correlation coefficients or boxplots describing the statistical association between the variables. On the lower triangle panel: factorial design plots or scatter plots describing the distribution of the values for each factorial combination of the variables (realized with the R function ‘ggpairs’ from the package {GGally}; (Schloerke et al. 2018)[1]).

---

[1] Schloerke, B., J. Crowley, D. Cook, F. Briatte, M. Marbach, E. Thoen, A. Elberg, and J. Larmarange. 2018. GGally: Extension to “ggplot2.”

Appendix S5. Summary figure of all the analyses proposed in the paper and appendices



Different methods for calculating beta diversity based on Hill numbers to assess the sensitivity of the conclusion to the method of beta calculation

Analysis 1 (main): Functional beta diversity patterns against null model of community keeping taxonomic beta diversity constant where beta diversity is calculated with the partititoning of **Rao's corrected index** (de Bello et al. 2010)

≠?

Analysis S10: Functional beta diversity patterns against null model of community keeping taxonomic beta diversity constant where several beta diversities are calculated with the **attribute-diversity approach** (Chao et al. 2019) by varying:

- The order of diversity, i.e. exponent of the Hill numbers (q=0,1,2), giving more or less weight to rare vs. common species
- The level of functional distinctiveness between species.

Patterns of functional beta diversity (β_{FD}) with respect to taxonomic beta diversity (β_{TD})

Potential assembly process induced

- Limiting similarity due to selection
- Competitive exclusion
- Local environmental heterogeneity
- *Facilitation*

- Stochastic with respect to traits
- Mix of divergence & convergence

- Habitat / environmental filtering
- *Weaker-competitor exclusion*

Analysis S9 : Variation partitioning of the taxonomic composition table (**no trait**) by **environmental & spatial predictors** as often used to disentangle potential niche vs. dispersal limitation effects on metacommunity structure (Peres-Neto et al. 2006)

Metacommunity mainly structured by dispersal limitation ("neutral")

Metacommunity mainly structured by environmental control ("niche")

≠?

Compare & assess whether metacommunities mainly structured by dispersal limitation are also the ones showing random trait patterns

Raw-data based approaches of beta diversity & trait-environment relationships

General conclusion:

Metacommunity processes unrelated to traits

Metacommunity processes related to traits

?

Assess the contribution of traits in the response of species composition to environment

Assembly patterns depending on environment are mostly unrelated to traits.

Assembly patterns depending on environment are mostly related to traits.

Compare the strength of response of taxonomic vs. functional beta diversity to environment with a distance-based approach

Analysis 2 (main): Functional beta diversity variation based on Hill numbers **in response to measured environmental variation**

% $\boldsymbol{\beta_{FD}}$ variation explained by environment variation

<

% $\boldsymbol{\beta_{TD}}$ variation explained by environment variation

% $\boldsymbol{\beta_{FD}}$ variation explained by environment variation

>

% $\boldsymbol{\beta_{TD}}$ variation explained by environment variation

($\boldsymbol{\beta_{TD/FD}}$=proportion of different équivalent taxonomic$_{TD}$/functional$_{FD}$ entities across sites)

Analysis S6 : Analysis of the taxonomic composition variation constrained by traits & environment with a double-CCA to quantify the contribution of trait composition in the community response to environment (ter Braak et al. 2018)

Analysis S7 : RLQ & Fourth-corner analyses to assess the nature and significance of trait-environment relationships (Dray et al. 2014)

Appendix S6. Complementary analysis on the contribution of traits to the variation of species composition across sites in response to environment – double-CCA approach

Overall, the percentage values of explained variation we obtained in the main analyses of the paper look particularly low. This is because distance-based approaches always give lower R2 than raw data-based approaches (Legendre and Fortin 2010, Legendre and Legendre 2012) due to the derived nature of distances (Tuomisto and Ruokolainen 2006). To have an idea of the relative importance of these figures, we can consider them with respect to the maximum variation that the environment could explain with this method, namely 32% (FBD) and 33% (TBD). Our conclusions remain essentially the same when using a raw-data based approach such as the double Constrained Correspondence Analysis (see below).

Rationale

One could argue that we may have underestimated the sensitivity of beta functional diversity to environment due to the method we used to a) calculate functional diversity, b) model the response of beta diversity to environmental variation.

To check our results' robustness to the calculation of functional diversity (a), we tried other traditional approaches (Kleyer et al. 2012) such as Community Weighted Means and RDA, convex hulls, and functional dispersion measures. All of them led us essentially to the same conclusion – functional diversity was in most cases less sensitive to the environment than taxonomic diversity. We kept de Bello's approach in the main analyses, because, contrary to the others: (i) It had received no criticism; (ii) It was adapted to our needs and hypotheses; (iii) It was recently recommended and properly validated (e.g. Chao et al. 2012); (iv) It is compatible with null modeling approaches (de Bello 2012), and cross-study comparisons (de Bello et al. 2010, Chao et al. 2012); and (v) It provided both total and pairwise versions of beta diversity.

See also why not using CWM-RDA approach when aiming to compare taxonomic and functional responses equitably (Peres-Neto et al. 2017).

In the main manuscript, we modelled non-linear responses of beta diversity to environmental variation (b) thanks to the combination of distance-based and GAM modelling. Other methods, such as hierarchical Joint Species Distribution Models (jSDMs), allow modelling complex relationships, and interactions between species, traits, and environment (Brown et al. 2014, Warton et al. 2015, Ovaskainen et al. 2016, Robroek et al. 2017). The main limitations of these methods currently are that they pre-suppose the existence of trait-environment relationships, they do not handle all types of data (abundances vs. presence/absences), some of them still lack flexibility, they are data-hungry, and sometimes computationally challenging (especially with multiple trait-environment combinations). In our case, they were not applicable on our datasets that had very different structures.

To check that the distance-based approach did not influence our conclusion, we applied a raw-data based approach that is more flexible than jSDMs; the double Constrained Correspondence Analysis (see below). In this case, the taxonomic composition is the fundamental level of information and the functional information explains a more or less important part of the variation of the taxonomic composition constrained by the environmental conditions. One of the advantages of the double CCA approach compared to other methods is that it is able to account for correlations among both environmental and trait variables (ter Braak et al. 2018).

Summary of the double CCA approach

This analysis studies the role of traits in the response of species composition to environment (Kleyer et al. 2012, ter Braak et al. 2018). The response is the raw beta diversity, i.e. the variation of species composition across sites (Legendre et al. 2005, 2008), instead of the variation of beta diversity as used in the distance-based approach (Tuomisto and Ruokolainen 2006, 2008).

Double CCA consists in constraining the species abundance matrix with the trait matrix before constraining it with the environment matrix. Thus, the fraction of species composition variation explained by environment when constrained by traits is always smaller than the fraction when no trait constraint is applied. Hence, this method assumes taxonomic diversity is always more, or at best equally informative as functional diversity. We applied the double-CCA analysis on the Hellinger-transformed species matrix, the orthonormalized environmental variables (representing 95% of the environmental data variation), and the orthonormalized traits (representing 95% of the trait data variation).

Raw data-based approaches are known to be particularly sensitive to the number of variables in the matrices (see Dray and Legendre 2008, Leibold and Chase 2017, Peres-Neto et al. 2017). Therefore, given the high heterogeneity of our datasets, we did not use it in the main study, but we here provide it as an exploration.

Results and conclusion

We first note that the percentages of total variation of species composition explained by environment obtained from the simple CCA of the species matrix with environment and without traits are well within the range of variation explained in other similar syntheses (e.g. Cottenie 2005, Soininen 2014), namely in average 31% (min = 5%, max 88%) (**Fig. S6.1**).

The double-CCA analysis (i.e. with the additional constraint of the trait matrix) further shows that, in average, **33% of the species composition explained by the environment would potentially be due to traits** (min=1%, median=26%, max=100%) (**Fig. S6.1**).

From the perspective that species diversity is always more informative than functional diversity (Petchey et al. 2004, Clark 2016), this analysis shows that traits composition can cover in most cases one third of the information that the species composition already covers.

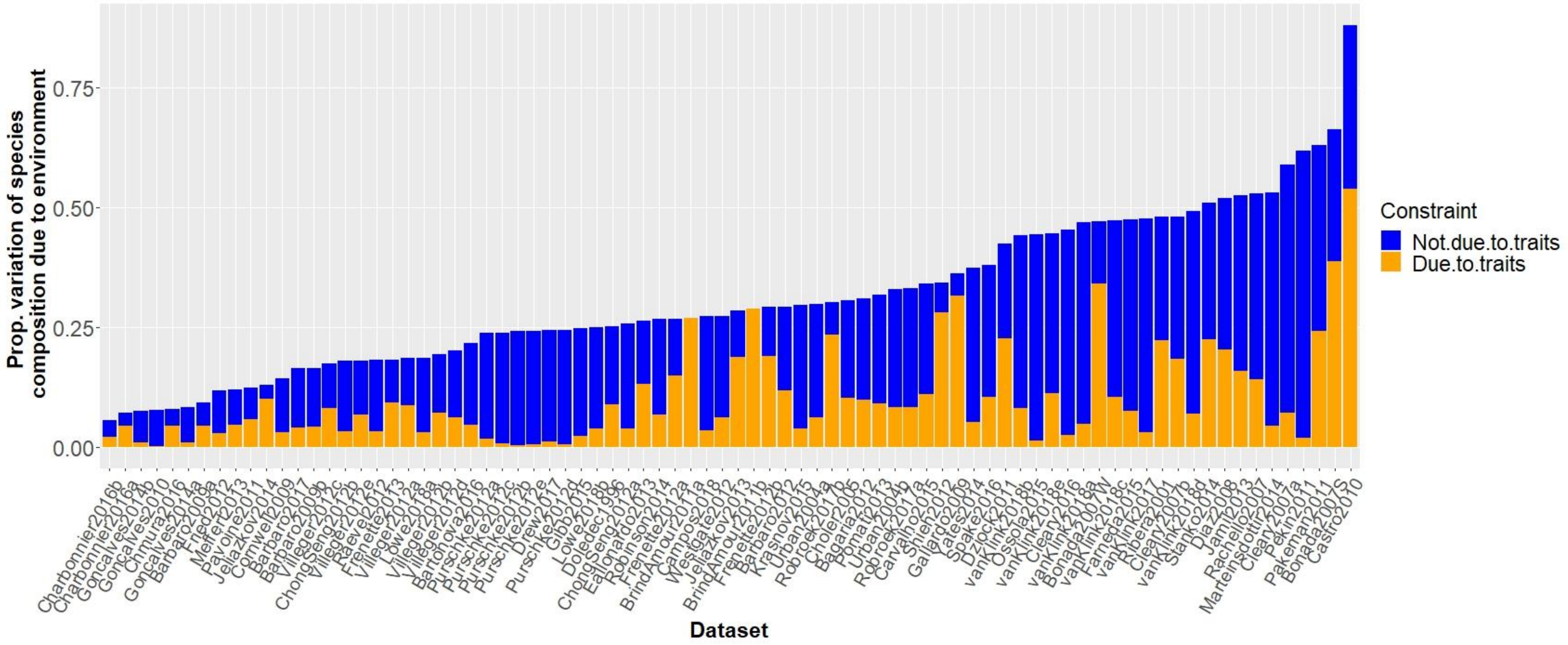


Figure S6.1. Proportion of species composition variation due to environment including the part of variation explained that is potentially due to the measured traits (orange) and the part that is not due to the measured traits (blue).

References

de Bello, F. 2012. The quest for trait convergence and divergence in community assembly: are null-models the magic wand? Global Ecology and Biogeography 21:312–317.

de Bello, F., S. Lavergne, C. N. Meynard, J. Lepš, and W. Thuiller. 2010. The partitioning of diversity: showing Theseus a way out of the labyrinth. Journal of Vegetation Science 21:992–1000.

ter Braak, C. J. F., P. Šmilauer, and S. Dray. 2018. Algorithms and biplots for double constrained correspondence analysis. Environmental and Ecological Statistics 25:171–197.

Brown, A. M., D. I. Warton, N. R. Andrew, M. Binns, G. Cassis, and H. Gibb. 2014. The fourth-corner solution – using predictive models to understand how species traits interact with the environment. Methods in Ecology and Evolution 5:344–352.

Chao, A., C.-H. Chiu, and T. C. Hsieh. 2012. Proposing a resolution to debates on diversity partitioning. Ecology 93:2037–2051.

Clark, J. S. 2016. Why species tell more about traits than traits about species: predictive analysis. Ecology 97:1979–1993.

Cottenie, K. 2005. Integrating environmental and spatial processes in ecological community dynamics. Ecology Letters 8:1175–1182.

Dray, S., and P. Legendre. 2008. Testing the Species Traits–Environment Relationships: The Fourth-Corner Problem Revisited. Ecology 89:3400–3412.

Kleyer, M., S. Dray, F. Bello, J. Lepš, R. J. Pakeman, B. Strauss, W. Thuiller, and S. Lavorel. 2012. Assessing species and community functional responses to environmental gradients: which multivariate methods? Journal of Vegetation Science 23:805–821.

Legendre, P., D. Borcard, and P. R. Peres-Neto. 2005. Analyzing beta diversity: partitioning the spatial variation of community composition data. Ecological Monographs 75:435–450.

Legendre, P., D. Borcard, and P. R. Peres-Neto. 2008. Analyzing or explaining beta diversity? comment. Ecology 89:3238–3244.

Legendre, P., and M.-J. Fortin. 2010. Comparison of the Mantel test and alternative approaches for detecting complex multivariate relationships in the spatial analysis of genetic data. Molecular Ecology Resources 10:831–844.

Legendre, P., and L. F. Legendre. 2012. Numerical ecology. Elsevier.

Leibold, M. A., and J. M. Chase. 2018. Metacommunity Ecology. Princeton University Press.

Ovaskainen, O., D. B. Roy, R. Fox, and B. J. Anderson. 2016. Uncovering hidden spatial structure in species communities with spatially explicit joint species distribution models. Methods in Ecology and Evolution 7:428–436.

Peres-Neto, P. R., S. Dray, and C. J. F. ter Braak. 2017. Linking trait variation to the environment: critical issues with community-weighted mean correlation resolved by the fourth-corner approach. Ecography 40:806–816.

Petchey, O. L., A. Hector, and K. J. Gaston. 2004. How Do Different Measures of Functional Diversity Perform? Ecology 85:847–857.

Robroek, B. J. M., V. E. J. Jassey, R. J. Payne, M. Martí, L. Bragazza, A. Bleeker, A. Buttler, S. J. M. Caporn, N. B. Dise, J. Kattge, K. Zając, B. H. Svensson, J. van Ruijven, and J. T. A. Verhoeven. 2017. Taxonomic and functional turnover are decoupled in European peat bogs. Nature Communications 8.

Soininen, J. 2014. A quantitative analysis of species sorting across organisms and ecosystems. Ecology 95:3284–3292.

Tuomisto, H., and K. Ruokolainen. 2006. Analyzing or explaining beta diversity? Understanding the targets of different methods of analysis. Ecology 87:2697–2708.

Tuomisto, H., and K. Ruokolainen. 2008. Analyzing or explaining beta diversity? reply. Ecology 89:3244–3256.

Warton, D. I., B. Shipley, and T. Hastie. 2015. CATS regression – a model-based approach to studying trait-based community assembly. Methods in Ecology and Evolution 6:389–398.

Appendix S7. Results from the RLQ and 4th corner analyses of the CESTES database

We applied the RLQ and fourth-corner analyses on the raw species, trait and environment data matrices (see R scripts for more information: https://doi.org/10.57745/LLBAZD).

For detailed information on the methods, please see the seminal papers:

- Dray, S., P. Choler, S. Dolédec, P. R. Peres-Neto, W. Thuiller, S. Pavoine, and C. J. F. ter Braak. 2014. Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. Ecology 95:14–21.
- Dray, S., and P. Legendre. 2008. Testing the species traits-environment relationships: the fourth-corner problem revisited. Ecology 89:3400–3412.

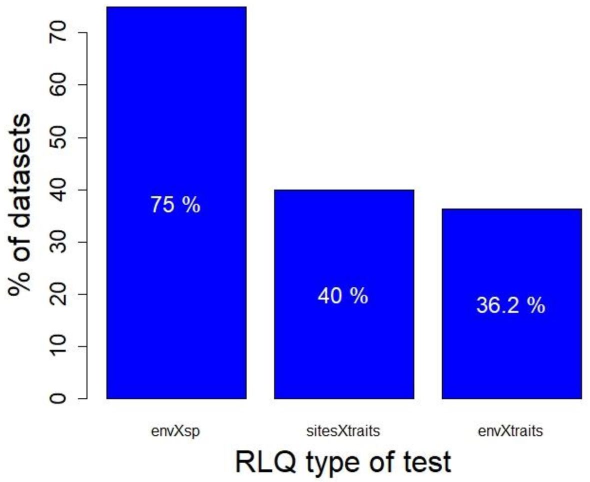


Figure S7.1. Proportion of datasets showing a generally significant RLQ relationship (see Dray et al. 2014); envXsp: significant relationship between Environment and Species; sitesXtraits: significant relationship between Sites and Traits; envXtraits: significant relationship between Environment and Traits. **36.2% of the datasets show a general significant link between traits and environment against 75%, between species and environment.**

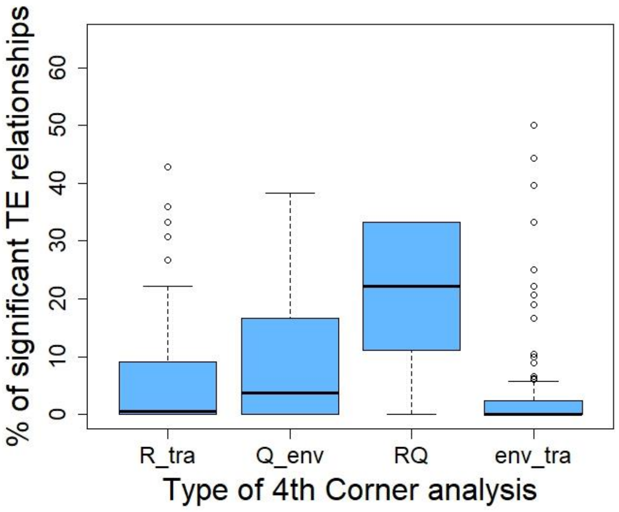


Figure S7.2. Distribution of the proportion of significant trait-environment relationships detected by Fourth-corner analyses across datasets after p-value correction (FDR) depending on the type of 4thcorner model tested, R_tra: relationship between environment gradients and individual trait variables, Q_env: relationship between trait syndromes and individual environmental variables, RQ: relationship between environment gradients and trait syndromes, env_tra: relationship between individual environmental variables and trait variables. **In the best case scenario in terms of explanatory power - i.e. when considering syndromes with gradients - in average 20% of the trait syndromes and environment gradients are significantly related.**

Appendix S8. Number and proportion of structuring traits across datasets and study groups

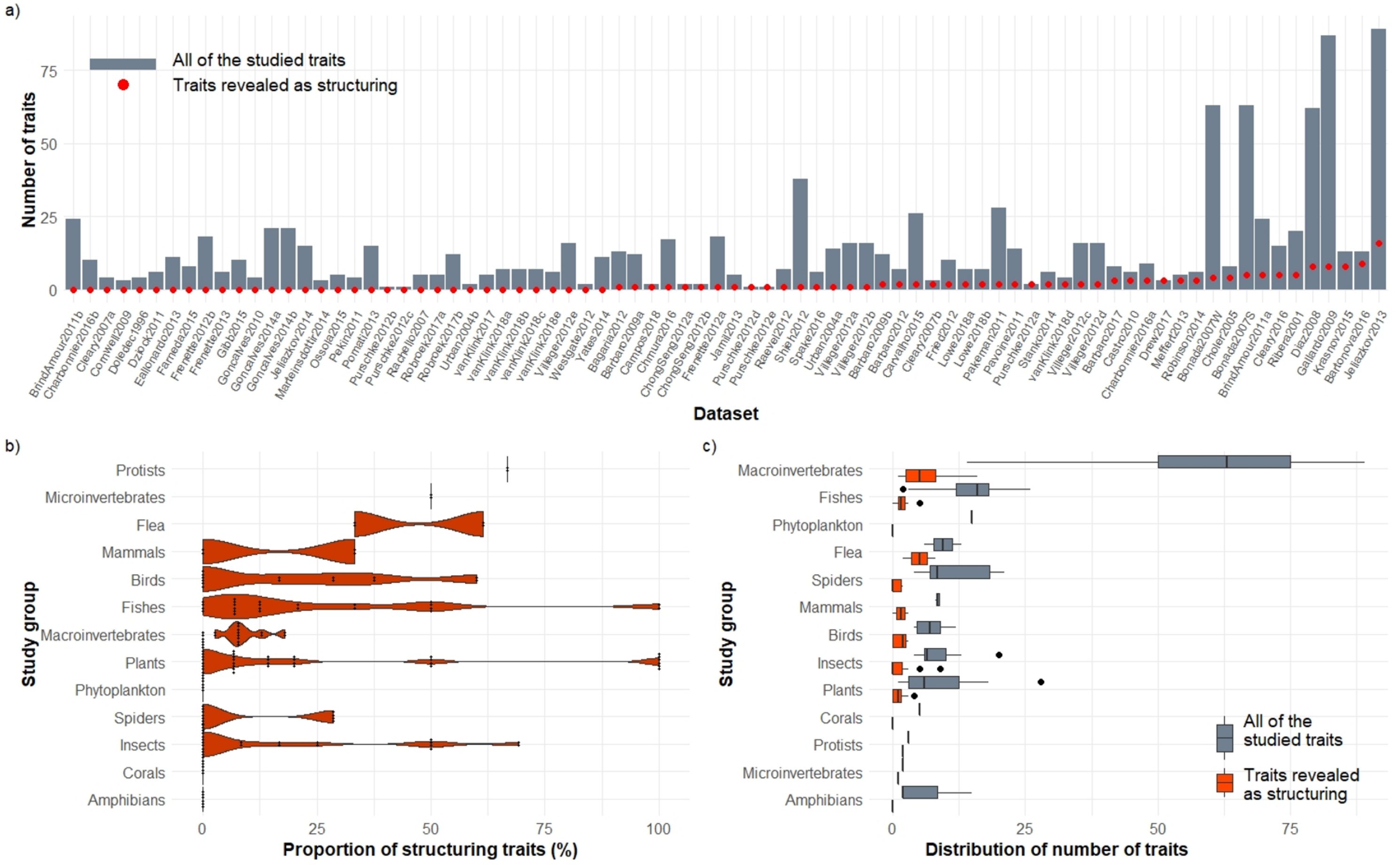


Figure S8.1. Distribution of structuring traits across datasets and study groups based on the multi-trait total functional turnover analysis. a) Total number of traits (grey bars), and number of traits that allows detecting significant trait dispersion (red dot) in each dataset; b) Proportion of structuring traits across study groups; c) Distribution of the total number of traits (grey boxplots), and of the number of traits allowing detecting significant trait dispersion (red boxplot) in each study group. Groupings in b) and c) based on (Jeliazkov et al. 2020).

Appendix S9. Are random patterns of traits evidence of neutral processes of metacommunities such as dispersal? Analysis of variation partitioning

Rationale

In our synthesis, we find that functional diversity explained metacommunity structure and response to environment in 25% of the datasets using multi-trait approach, and up to 59% using single-trait approach with 19%±27% of the traits showing significant signal. In most situations and for all types of traits, we find that trait diversity structure is mainly random with respect to taxonomic diversity (see the figures of the main MS). We conclude that in most situations and for a majority of traits, trait diversity does not improve our ability to infer metacommunity processes compared to taxonomic diversity alone.

However, some could interpret this absence of signal as the signature of stochastic processes of metacommunity structuring, such as dispersal (e.g. de Bello et al. 2013). Although we do not think, an absence of signal should be treated as an evidence of the existence of an effect, we found this assumption interesting and worth investigating further.

Therefore, we re-analysed each of the CESTES dataset and addressed the following question: Are the metacommunities that show random trait patterns more likely dominated by dispersal processes?

Summary of the applied method of variation partitioning

To address our question, we used a classical variation partitioning approach that allows estimating the relative importance of space vs. environment in metacommunity structuring. The method of variation partitioning has widely been used to assess the relative contribution of niche vs. dispersal effects in metacommunity studies (e.g. Cottenie 2005, Soininen 2014, 2016). However, this approach has strong and well-recognized limitations (e.g. Smith and Lundholm 2010, Gilbert and Bennett 2010, Viana et al. 2022) and it is not yet adapted to a trait-based analysis, making hard to compare functional with taxonomic diversities. Therefore, we did not use it for the main manuscript. However, to explore the above-mentioned assumption in our context of synthesis and post-hoc interpretation, it was the most straightforward approach.

For each of the 80 CESTES datasets, we used the RDA-based variation partitioning on the Hellinger transformed **community table** (Legendre and Gallagher 2001, Legendre and Legendre 2012) in response to the **environment table** (orthonormal components from a Principal Component Analysis of the environmental variables) and to the **space table** (Moran Eigenvector Maps derived from a relative neighbour graph with binary weights) (for more details on these classical approaches, see e.g. Peres-Neto et al. 2006, Dray et al. 2006, 2012, Soininen 2014, Bauman et al. 2018). A forward selection procedure (999 permutations) was applied on both environment and space matrices to select only relevant variables and avoid variation inflation. We further used the Moran Spectral Randomization correction to avoid spurious correlations between environment and space (Clappe et al. 2018). We then extracted the pure spatial fraction (i.e. the effect of space only, once environmental effect is removed) as the potential signature of dispersal effects.

Finally, to test whether dispersal processes more likely dominated the metacommunities that expressed random trait patterns in the main analysis, we plotted the distribution of the pure spatial fraction against the types of trait pattern revealed by the trait analyses. We tested the difference significance with Kruskall-Wallis rank sum test.

Results and conclusion

According to the variation partitioning analysis, metacommunities in the CESTES database are slightly more driven by dispersal than by environment (in average, [E] = 0.07 ± SD 0.06 VS. [S] = 0.11 ± SD 0.10) but this is highly variable across datasets (**Fig. S9.1**).

However, the metacommunities showing random trait patterns (see main MS) are not significantly more driven by dispersal limitation than the others (**Fig. S9.2**). Moreover, there are several metacommunities highly responsive to space that yet show significant trait structuring, either divergence or convergence (**Fig. S9.2**). These results suggest that in these metacommunities, the randomness of trait diversity with respect to taxonomic diversity is not necessarily the evidence of dispersal limitation dominancy.

To conclude, it seems that in this synthesis, the observed trait diversity randomness is not more the proof of neutral dynamics dominancy - namely dispersal, in this case - than of current trait-based approach difficulty to capturing metacommunity complexity.

To go further, one would need to test the importance of ecological drift (which is another source of stochasticity in metacommunities (e.g. Vellend 2010)) in the datasets and determine whether this could explain the majority of trait dispersion randomness observed, but this seems difficult to test with these data.

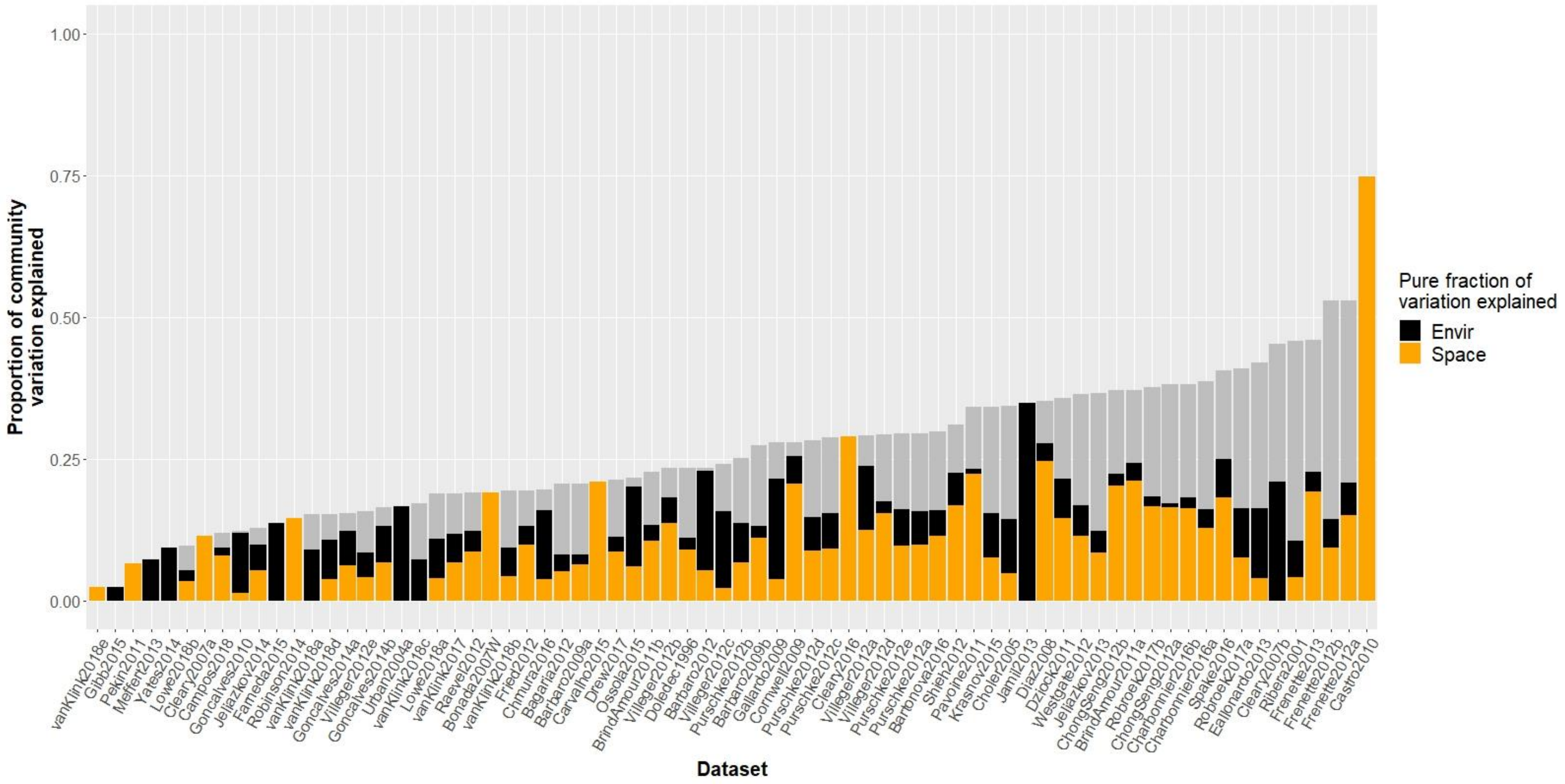


Figure S9.1. Results from the variation partitioning applied on each of the CESTES datasets. Total variation explained (grey) and pure fractions of environment (black) and space (orange) are represented.

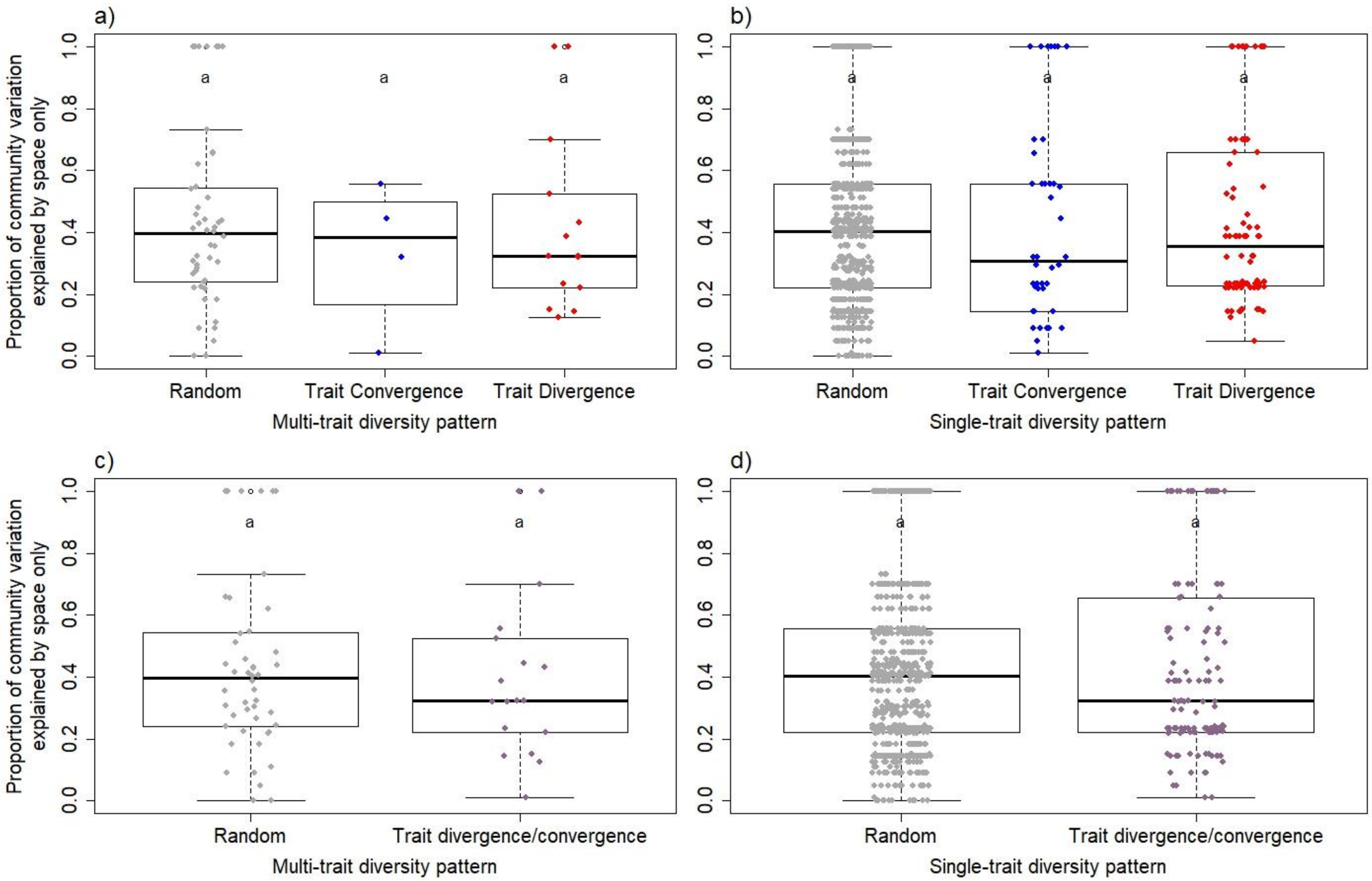


Figure S9.2. Links between trait diversity patterns and strength of the signature of dispersal dominance observed in the CESTES metacommunities. Upper panels: analysis separating trait divergence and convergence. Lower panels: analysis pooling both significant trait structures, for (a,c) multi-trait diversity analysis, and (b,d) single-trait analysis. No significant difference was found. (a) Kruskal-Wallis chi-squared = 0.12213, df = 2, p-value = 0.9408; b) Kruskal-Wallis chi-squared = 0.32997, df = 2, p-value = 0.8479; c) Kruskal-Wallis chi-squared = 0.11971, df = 1, p-value = 0.7294; d) Kruskal-Wallis chi-squared = 0.030917, df = 1, p-value = 0.8604).

References

Clappe, S., S. Dray, and P. R. Peres-Neto. 2018. Beyond neutrality: disentangling the effects of species sorting and spurious correlations in community analysis. Ecology 0.

Cottenie, K. 2005. Integrating environmental and spatial processes in ecological community dynamics. Ecology Letters 8:1175–1182.

de Bello, F., M. Vandewalle, T. Reitalu, J. Lepš, H. C. Prentice, S. Lavorel, and M. T. Sykes. 2013. Evidence for scale- and disturbance-dependent trait assembly patterns in dry semi-natural grasslands. Journal of Ecology 101:1237–1244.

Dray, S., P. Legendre, and P. R. Peres-Neto. 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecological Modelling 196:483–493.

Dray, S., R. Pélissier, P. Couteron, M.-J. Fortin, P. Legendre, P. R. Peres-Neto, E. Bellier, et al. 2012. Community ecology in the age of multivariate multiscale spatial analysis. Ecological Monographs 82:257–275.

Gilbert, B., and J. R. Bennett. 2010. Partitioning variation in ecological communities: do the numbers add up? Journal of Applied Ecology 47:1071–1082.

Legendre, P., and E. D. Gallagher. 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129:271–280.

Legendre, P., and L. F. Legendre. 2012. Numerical ecology (Vol. 24). Elsevier.

Peres-Neto, P. R., P. Legendre, S. Dray, and D. Borcard. 2006. Variation Partitioning of Species Data Matrices: Estimation and Comparison of Fractions. Ecology 87:2614–2625.

Smith, T. W., and J. T. Lundholm. 2010. Variation partitioning as a tool to distinguish between niche and neutral processes. Ecography 33:648–655.

Soininen, J. 2014. A quantitative analysis of species sorting across organisms and ecosystems. Ecology 95:3284–3292.

Soininen, J. 2016. Spatial structure in ecological communities – a quantitative analysis. Oikos 125:160–166.

Vellend, M. 2010. Conceptual Synthesis in Community Ecology. The Quarterly Review of Biology 85:183–206.

Viana, D. S., P. Keil, and A. Jeliazkov. 2022. Disentangling spatial and environmental effects: Flexible methods for community ecology and macroecology. Ecosphere 13:e4028.

Appendix S10. Supplementary analysis on the role of functional diversity in inferring metacommunity processes – Chao's approach

Rationale

In the main analyses, we used the biodiversity partitioning approach proposed by de Bello (2010) which is based on Rao's quadratic entropy. Such a Rao-based framework has several important advantages and unique properties allowing comparison across different diversity facets and study ecosystems within a single framework (de Bello et al. 2010, Chao et al. 2012).

By using this framework to calculate functional beta diversity, our main analyses detected significant turnover of functional strategies (either lower or higher than expected given the taxonomic turnover) in only 25% of the datasets. We concluded that the role of trait diversity in inferring metacommunity processes might be more limited than expected given the enthusiasm towards trait-based community ecology.

Nevertheless, one could argue that we may have underestimated the ability of functional beta diversity analysis to uncover patterns of functional turnover due to the method we used. In particular, a new approach was recently proposed as potentially able to bring further insights: the attribute-diversity approach to functional diversity (Chao et al. 2019). Thus, we here provide a supplementary analysis based on this approach in order to compare our results and put them in perspective.

Summary of the attribute-diversity approach to functional diversity

The approach proposed by Chao et al. (2019) is based on Rao's quadratic entropy and thus has many commonalities with de Bello's approach (de Bello et al. 2010) we used in the main analyses. They are both based on the effective number of species/functional entities ("species-equivalent").

The main difference is that Chao's approach proposes to explore not only one given beta diversity value for every dataset but a range of diversity values ("diversity profiles") by varying two parameters: a) the order of diversity (q={0, 1, 2}; depending on how strong the common vs. rare species are weighted by their abundances), and b) the threshold of species distinctiveness (tau ∈ [dmin, dmax]; depending on the threshold used for the functional clustering of the species).

In order to ease the comparison of several beta diversity profiles across many datasets, the authors suggest exploring at least the following combinations of parameters *q={0, 1, 2}* x *tau={dmin, dmean, dmax}* where:

- *q=0* implies that every species has the same weight in the calculation of the index (in the case of taxonomic diversity, this index equates the species richness).
- *q=1* implies weighting each species in proportion to its abundance (with a geometric average) in the calculation of the index (in the case of taxonomic diversity, this index equates the Shannon entropy index).
- *q=2* implies weighting each species in proportion to its abundance (with an arithmetic average) in the calculation of the index, giving disproportionately more weight to dominant species (in the case of taxonomic diversity, this index equates the Simpson index).
- *tau=dmin* is the minimum (functional) distance between all the species of the metacommunity and is used as the threshold from which two species are considered as distinct in the calculation

of the index; in this case, the index is considered as the taxonomic diversity (but see comment below)

- *tau=dmean* is the mean functional distance between all the species of the metacommunity and is used as the threshold from which two species are considered as distinct in the calculation of the index; in this case, the index is considered as a functional diversity with intermediate functional clustering criteria
- *tau=dmax* is the maximum functional distance between all the species of the metacommunity and is used as the threshold from which two species are considered as distinct in the calculation of the index; in this case, the index is considered as a functional diversity with coarser functional clustering criteria.

The functional diversity index we used in the main analysis based on de Bello's approach is supposed to correspond to the combination of {q=2; tau=dmax}. The suggestion of Chao's & coll. is to explore not only this combination but also all the other ones based on the parameter values given above.

It is important to note that, in their 2019 paper, Chao & coll. seem to consider taxonomic diversity as a special case of functional diversity and even name it "functional diversity" (see e.g., Chao et al. 2019: Figure 2b). This is also reflected in their code. They calculate their *taxonomic* diversity by using the *trait*-based Gower distance matrix and consider the minimal functional distance (dmin) as a threshold of species distinctiveness. They do not use the taxonomic classification as we normally do with Rao-based frameworks, i.e. considering a constant distance of 1 between species (see all the relevant works from Pavoine, de Bello, Ricotta, etc.). Therefore, we have to keep in mind that using Chao's framework here makes us compare taxonomic and functional diversity in a slightly different way than we did it through de Bello's framework in the main analysis.

We used and adapted the R script provided in Chao & coll.'s Supp. Mat to calculate their suggested measures of taxonomic and functional beta diversity.

In order to test our ability to draw inferences about metacommunity processes (habitat filtering vs. biotic sorting) with these newly calculated measures of functional diversity, we followed exactly the same procedure as the one used in the main analyses. We applied an unconstrained trait-shuffling algorithm that consists in permuting species labels across the species trait matrix while the species abundance/presence-absence matrix remains unchanged; this was repeated 500 times (instead of 1000 times because it already took 3.6 days to run). This algorithm ensures that the species abundance/presence-absence matrix keeps the same spatial structure and species richness while the species-traits links are shuffled. For each newly generated trait matrix, we calculated taxonomic and functional beta diversities based on Chao's approach. Because the distribution of the beta diversity indices calculated on the null reference data were not distributed normally in most of the cases, we log transformed the values of these indices for both the observed and null-based indices (Botta-Dukát 2018). To assess the significance of trait convergence vs. divergence, we calculated the Standardized Effect Size (Gotelli and McCabe 2002) on these log transformed values (Swenson 2014) for each dataset: $SES\ FBD = (logFBD_{obs} - mean(logFBD_{null})) / sd(logFBD_{null})$ (for more information on the SES, see the *Methods* section of the paper).

Results and discussion

As a reminder, in the main analyses based on de Bello's approach, we had found that, among the 80 datasets, most (60 out of 80) did not differ from random expectations with respect to the co-occurrence of species with different traits; only **25%** showed a functional turnover that was significantly different from expected given the taxonomic turnover (main manuscript: **Fig. 2**).

In the following, we compare this result to the new results based on the attribute-diversity approach to functional diversity proposed by Chao et al. (2019).

First, we notice that with the combination {q=2, tau=dmax} (**Fig. S10.1**, third panel from the left) - that is supposed to be equivalent to our original approach - we find significant functional turnover in 13 datasets out of the 80, that is **16%** of the studies (11 datasets showing high turnover and 2 datasets showing low turnover). Even though these 13 datasets were also identified as structured by the original approach (they are part of the 20), the results quite differ with 10% less datasets identified compared to de Bello's approach. Consequently, we suspect the Chao's approach not to be strictly equivalent as soon as we compare the null communities-based functional diversities to *this taxonomic diversity*. Another reason for this discrepancy may be that many of the null distributions of functional beta diversity across tau x q combinations showed strongly non-normal distribution. Thus, in some cases, even the log-transformation probably failed in ensuring a safe SES test (Botta-Dukát 2018).

Second, when considering all of the combinations of tau and q, we find in total 38 datasets out of the 80 that show a significant functional turnover in at least one tau-q combination, that is **47.5%** of the datasets. This is an undoubtedly higher number than the one we found with the original approach that considers only one tau-q combination. It is however expected since in the original approach, the functional diversity is calculated based on the extreme side of the tau-q gradient (where both q and tau are set at their maximum value). As one decreases tau, one increasingly refines the resolution of the functional grouping until the point where one functional group is simply equivalent to one (taxonomic) species. Doing so, the functional diversity becomes closer and closer to the taxonomic diversity, which makes functional diversity more and more able to show significant structure compared to taxonomic diversity. This result complements our main results. It shows that unless functional diversity is calculated with a fine resolution close to the taxonomic resolution, it allows inferring metacommunity processes in only a limited number of cases. Using the mean species functional distance as a threshold of species distinctiveness instead of the maximum distance substantially improves this (35 datasets with dmean vs. 23 datasets dmax, considering all q together).

Third, and more interestingly, the datasets that show a significant functional turnover differ depending on the value of q. In general, **35%** of the datasets show significant turnover when considering all of the three possible values of q. This is due to differences among datasets in their species abundance distributions, and thus, in the role of common species in driving diversity patterns. For instance, datasets that have a very skewed species abundance distribution with a lot of rare species will be more properly analyzed with q=0 and our ability to detect significant functional turnover may be enhanced. This is more a question of optimal calibration of the diversity index on a case-by-case basis. One would first have to define which q is the best for each study and then use it for the calculation of the functional diversity. Given tau=dmax, decreasing q makes functional diversity less able to detect significant functional turnover, with 5 cases for q=0, 17 cases for q=1, and 13 (Chao)/20 (de Bello) cases for q=2. Thus, the q we used in our original analyses (q=2) based on de Bello's approach was still the one that affected the least our ability to detect significant structure in functional turnover. Therefore, when considering the functional distance threshold tau=dmax, and the species weighting scheme of q=2, we did not substantially affect our ability to detect significant structure in functional turnover compared to other parameter choices. In addition, using the same q=2 to calculate both taxonomic and functional diversity allow comparing taxonomic and functional diversity on the same level. Our general conclusion would have been at least qualitatively the same whatever q. Of course, we could draw new particular conclusions with respect to differences among datasets, and other singularities. However, this is not the scope of the main paper, which is about synthesizing and trying to find generality among classical trait-based studies.

Perspectives

Chao’s framework undoubtedly brings precious insights into trait-based analyses, especially on a case-by-case basis, when trait information is limited and species abundance distribution is skewed (species-rich assemblages). However, there are still some grey areas and points to develop in order to make it applicable in a synthesis context.

First, it would be interesting to know more about the biological hypotheses underlying specific choice of threshold of species distinctiveness and how such choices link to the *traditional* taxonomic diversity (i.e. based on a species classification that does not rely on any functional information). This is particularly important when considering that taxonomic diversity can encompass a lot more of ecological information than functional diversity (Clark 2016). Second, it would be valuable to better link this new framework with the existing de Bello’s framework and harmonize approaches. In particular, Chao’s approach does not provide yet any formulation for the pairwise equivalent of their beta diversity which is however very useful for modeling diversity-environment relationships. Even though it would be, by principle, possible to calculate, we do not know yet the properties of such an index. It would be good to explore these before applying it on different datasets in a synthesis context. Third, some validation steps are needed with respect to the use of null modeling approaches in Chao’s framework, including checking the effect of q and tau on the normality of beta diversity measures, and clarifying which taxonomic diversity should be used in the SES test (the traditional one, or the one based on the minimum Gower distances?). Fourth, although Chao’s R function is supposed to deal with presence-absence data when the user sets the argument right, it currently does not work and returns error messages. Fifth, the function does not work when there is perfect functional redundancy in the dataset, that is, when several species have exactly the same traits with same trait values. We had to adapt the code in order to make it work with some of our datasets that had this particular feature. This is also, why we think that the way the taxonomic diversity is defined in Chao’s framework would deserve some clarification within the grasp of the end users. An extended validation of the R function would certainly be useful for further applications.

To conclude, although such approaches are promising, they need further validation for synthetic work, in particular with respect to the cross-study comparability, the way taxonomic diversity is defined, the biological hypotheses underlying the index calculation and the properties of the generated indices.

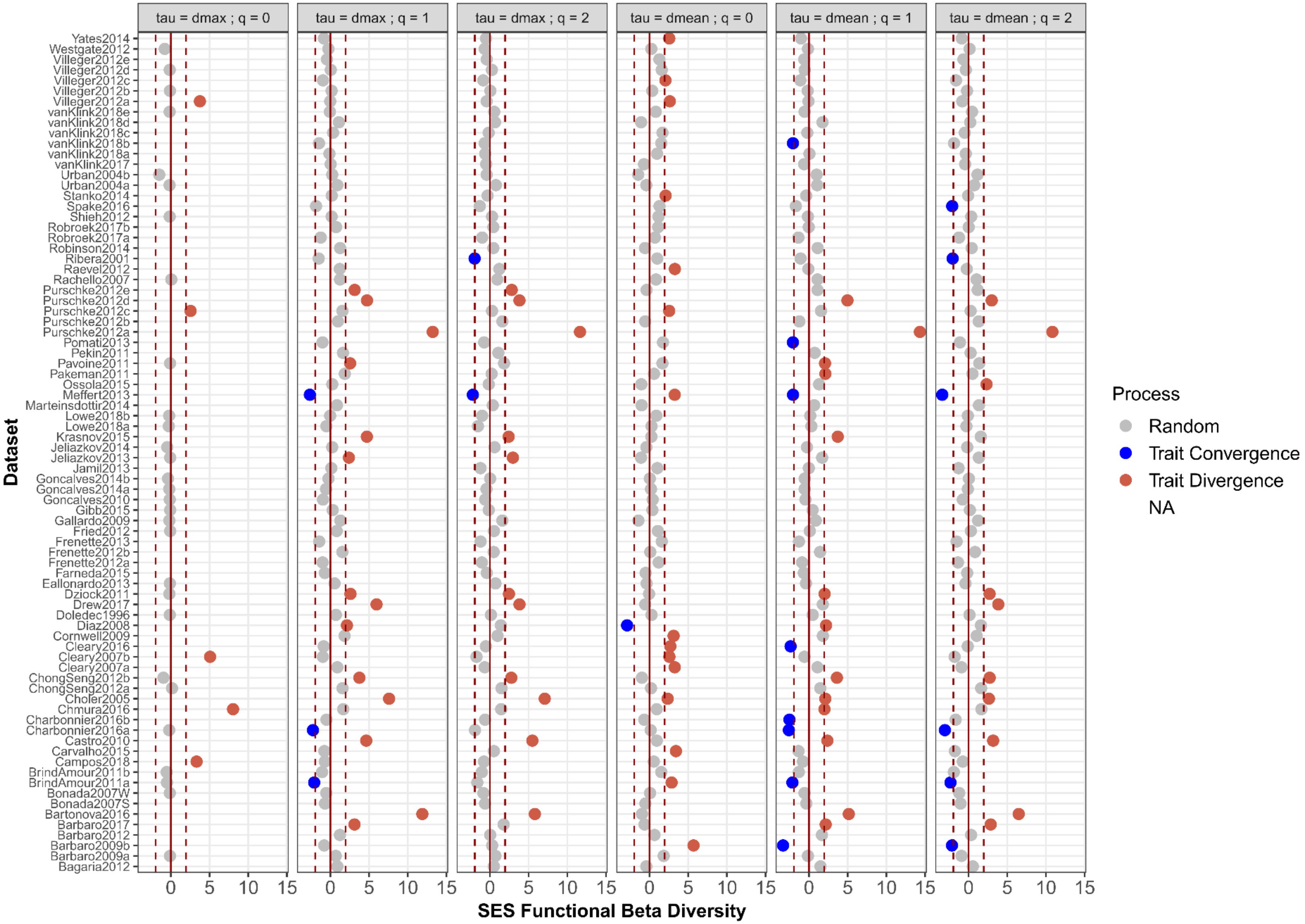


Figure S10.1. Trait-related determinism in metacommunity structure based on the attribute-diversity approach. Plots of the Standardized Effect Size (SES) of the total functional beta diversity for each dataset showing in which cases the overall functional turnover is lower (blue dots), or higher (red dots) than expected, or random (grey dots), given the taxonomic turnover, for every relevant combination of q and tau (except combinations including dmin since they are used as the taxonomic diversity). For some datasets and parameter combinations, the SES was not calculable; hence, some dots are absent from the figure.

References

de Bello, F., S. Lavergne, C. N. Meynard, J. Lepš, and W. Thuiller. 2010. The partitioning of diversity: showing Theseus a way out of the labyrinth. Journal of Vegetation Science 21:992–1000.

Botta-Dukát, Z. 2018. Cautionary note on calculating standardized effect size (SES) in randomization test. Community Ecology 19:77–83.

Chao, A., C.-H. Chiu, and T. C. Hsieh. 2012. Proposing a resolution to debates on diversity partitioning. Ecology 93:2037–2051.

Chao, A., C.-H. Chiu, S. Villéger, I.-F. Sun, S. Thorn, Y.-C. Lin, J.-M. Chiang, and W. B. Sherwin. 2019. An attribute-diversity approach to functional diversity, functional beta diversity, and related (dis)similarity measures. Ecological Monographs 89:e01343

https://doi.org/10.1086/727471.

Appendix S11. Role of sampling and ecological contexts in the Relative Sensitivity of pairwise Functional Beta Diversity to environment

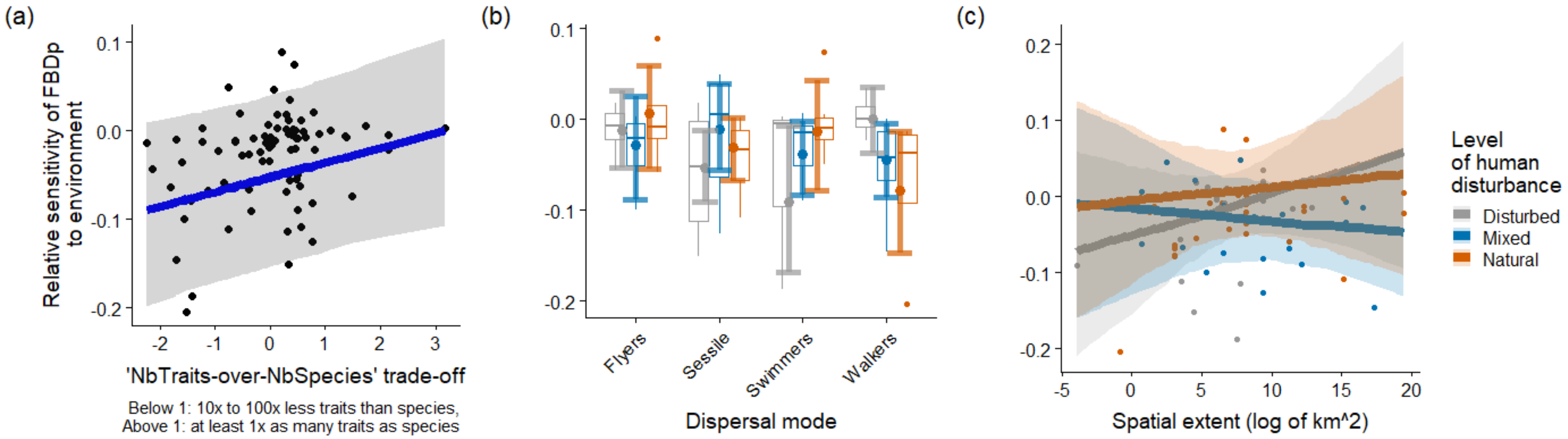


Figure S11.1. Relative sensitivity of pairwise functional beta diversity (FBDp) to environment as predicted by the final synthesis model depending on three potentially influent predictors, namely a) traits-species trade-off (increasing number of traits at the expense of number of species), b) interaction between dispersal mode and level of human disturbance, and c) interaction between level of human disturbance and scale of study. Small dots (a, c) and boxplots (b) are the raw data; lines (a, c) and big dots (b) are the means predicted by the model (marginal effects); the envelopes (a, c) and the interval whiskers (b) are the 95% posterior confidence interval.

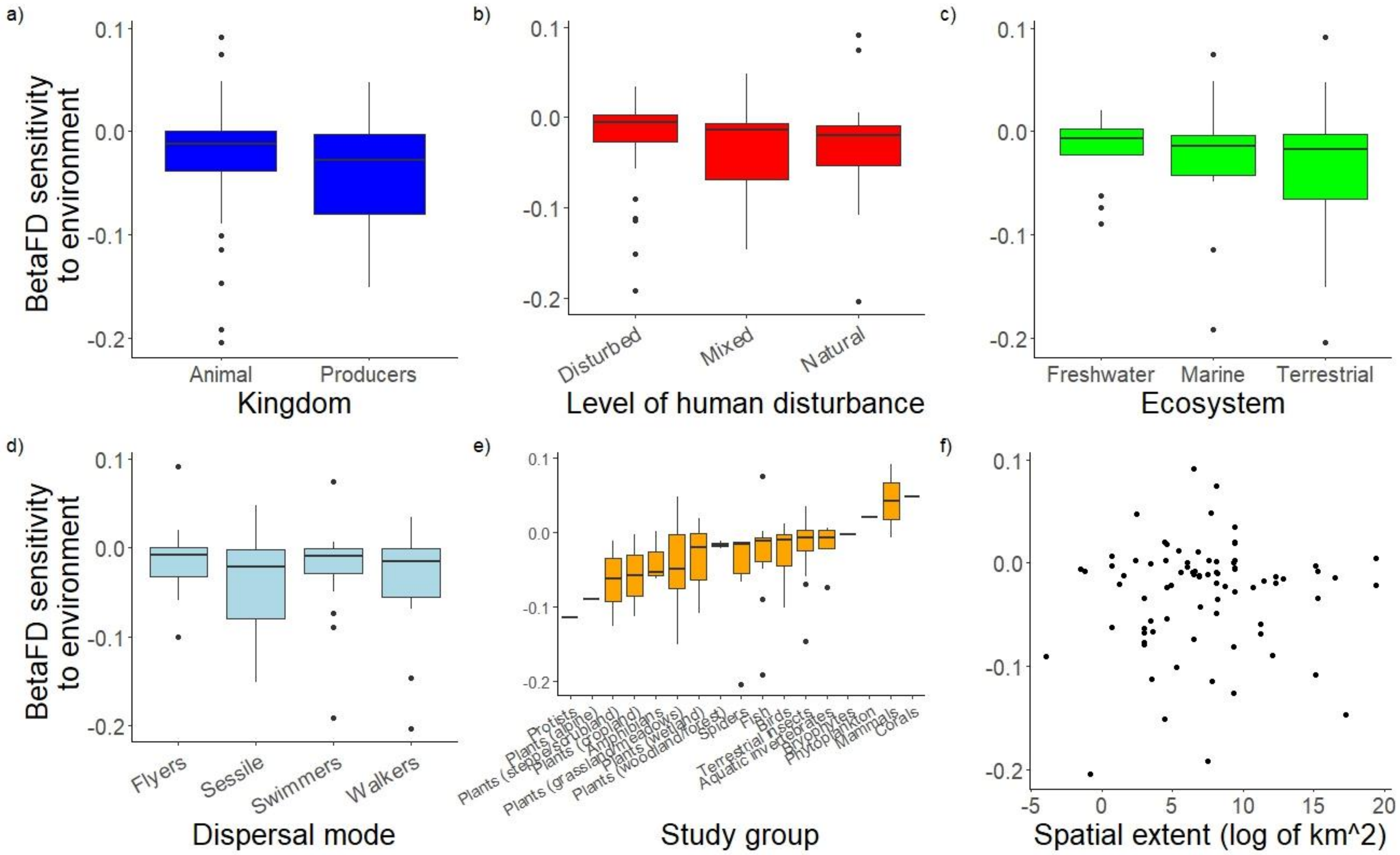
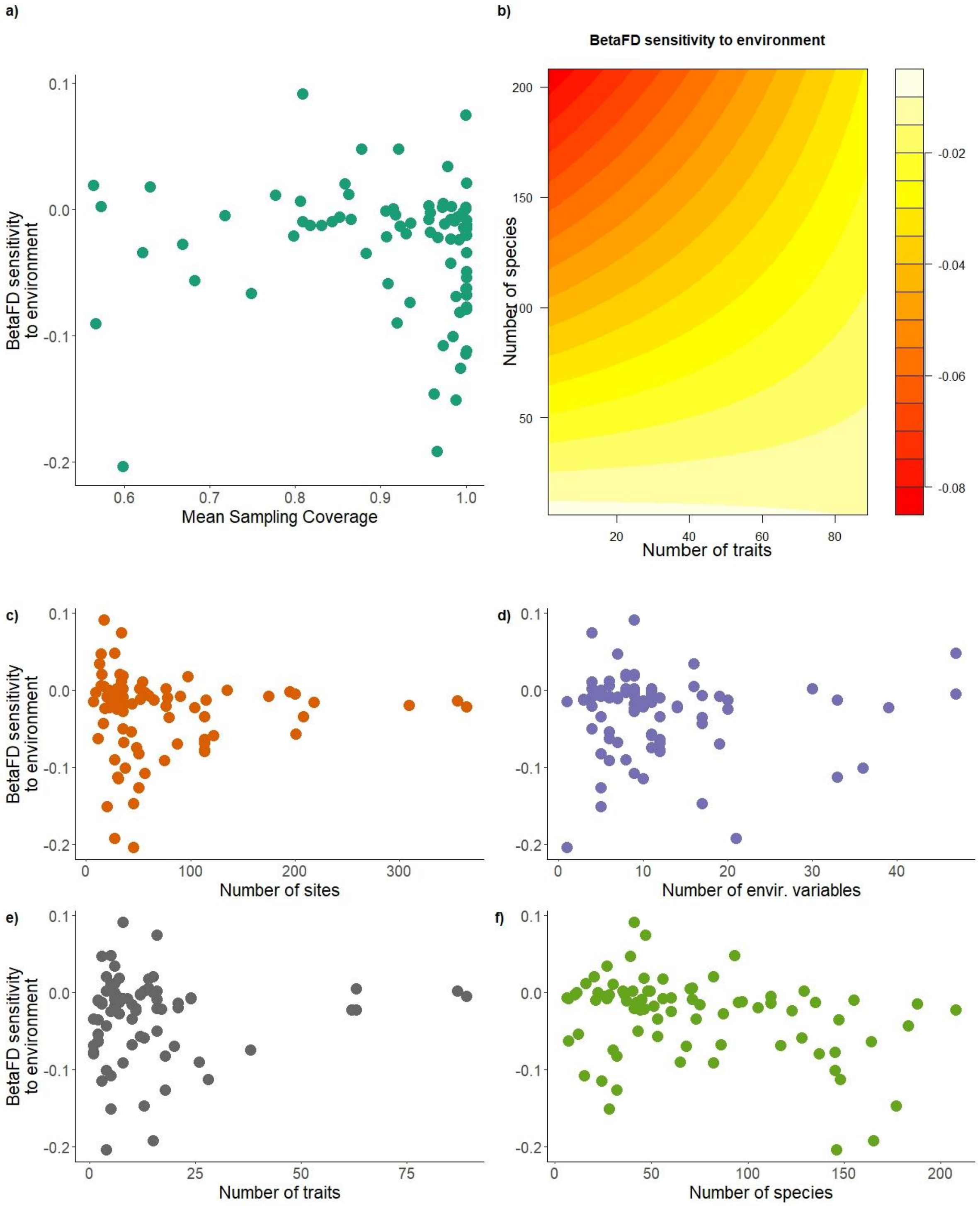
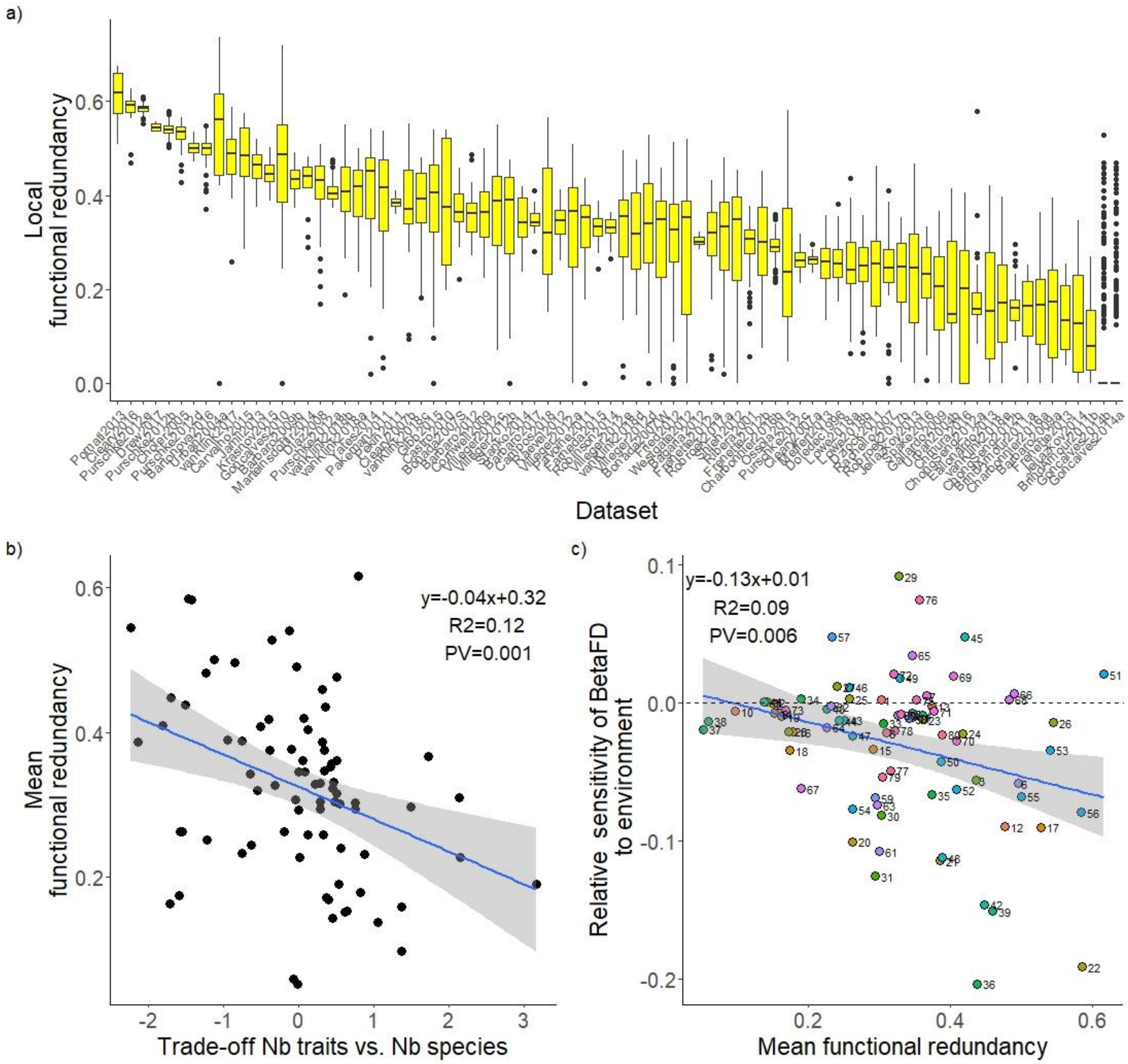


Figure S11.2. Exploration plots (raw data) of the relationship between the relative sensitivity of functional pairwise beta diversity (BetaFD=FBDp) and the different ecological features of the datasets, namely the a) kingdom (simplified to two levels), b) level of disturbance, c) ecosystem type, d) dispersal mode, e) study group, and f) spatial extent of the study.



FigureS11.3. Exploration plots of the relationship between the relative sensitivity of functional beta diversity (BetaFD=FBDp) and different sampling properties of the datasets, namely a) mean sampling coverage, b) trade-off between the number of traits and number of species, c) number of sampling sites, d) number of environmental variables, e) number of traits, and f) number of species of the datasets.



1. Bagaria2012, 2. Barbaro2009a, 3. Barbaro2009b, 4. Barbaro2012, 5. Barbaro2017, 6. Bartonova2016, 7. Bonada2007S, 8. Bonada2007W, 9. BrindAmour2011a, 10. BrindAmour2011b, 11. Campos2018, 12. Carvalho2015, 13. Castro2010, 14. Charbonnier2016a, 15. Charbonnier2016b, 16. Chmura2016, 17. Choler2005, 18. ChongSeng2012a, 19. ChongSeng2012b, 20. Cleary2007a, 21. Cleary2007b, 22. Cleary2016, 23. Cornwell2009, 24. Diaz2008, 25. Doledec1996, 26. Drew2017, 27. Dziock2011, 28. Eallonardo2013, 29. Farneda2015, 30. Frenette2012a, 31. Frenette2012b, 32. Frenette2013, 33. Fried2012, 34. Gallardo2009, 35. Gibb2015, 36. Goncalves2010, 37. Goncalves2014a, 38. Goncalves2014b, 39. Jamil2013, 40. Jeliazkov2013, 41. Jeliazkov2014, 42. Krasnov2015, 43. Lowe2018a, 44. Lowe2018b, 45. Marteinsdottir2014, 46. Meffert2013, 47. Ossola2015, 48. Pakeman2011, 49. Pavoine2011, 50. Pekin2011, 51. Pomati2013, 52. Purschke2012a, 53. Purschke2012b, 54. Purschke2012c, 55. Purschke2012d, 56. Purschke2012e, 57. Rachello2007, 58. Raevel2012, 59. Ribera2001, 60. Robinson2014, 61. Robroek2017a, 62. Robroek2017b, 63. Shieh2012, 64. Spake2016, 65. Stanko2014, 66. Urban2004a, 67. Urban2004b, 68. vanKlink2017, 69. vanKlink2018a, 70. vanKlink2018b, 71. vanKlink2018c, 72. vanKlink2018d, 73. vanKlink2018e, 74. Villeger2012a, 75. Villeger2012b, 76. Villeger2012c, 77. Villeger2012d, 78. Villeger2012e, 79. Westgate2012, 80. Yates2014

Figure S11.4. Functional redundancy in the datasets; a) distribution of the local functional redundancy calculated with the R function ‘rao.diversity’ from the package {SYNCSA} (Debastiani and Pillar 2012)[2], b) link between the mean functional redundancy of the dataset and the trade-off between the number of traits and the number of species used in the studies, and c) link between the relative sensitivity of Functional Beta Diversity to environment and the mean functional redundancy in the datasets. **These plots suggest that the local functional redundancy might play a negative role in the sensitivity of**

---

[2] Debastiani, V., and V. Pillar. 2012. SYNCSA - R tool for analysis of metacommunities based on functional traits and phylogeny of the community components. Bioinformatics 28:2067–2068.

Functional Beta Diversity to environment. We should capture this effect by using the trade-off between number of traits and number of species as a predictor in the final synthesis model.

Appendix S12. Statistical results from the BRMS model

Table S12.1. Output tables from the BRMS meta-analysis model with the relative sensitivity of the pairwise Functional Beta Diversity (FBDp) to environmental variation as response, level of human disturbance (three levels of “hemeroby”: Disturbed, Mixed, Natural), dispersal mode (four levels: Flyers, Walkers, Swimmers, Sessile), spatial scale (extent), number of environmental variables, trade-off between number of species and traits, and sample size as predictors, and study identifier as random intercept effect. Conditional R squared of the model: R2=0.6755496 (Estimate error=0.1074983, Q2.5=0.4378981, Q97.5=0.8359284).

Model parameter	**Effect tested**	**mean**	**se_mean**	**sd**	**perc2.5**	**perc25**	**perc50**	**perc75**	**perc97.5**	**n_eff**	**Rhat**
b_Intercept	Intercept(Disturbed/Flyers)	-0.01	0	0.02	-0.05	-0.03	-0.01	0	0.03	540	1
b_Hemeroby_3Mixed	Level of disturbance	-0.02	0	0.04	-0.09	-0.04	-0.02	0.01	0.05	566	1
b_Hemeroby_3Natural	Level of disturbance	0.02	0	0.04	-0.06	-0.01	0.02	0.04	0.08	653	1
b_scaleExtent_km2_log	Spatial scale	0.03	0	0.03	-0.03	0.01	0.03	0.04	0.08	569	1
b_DispSimpl2Sessile	Dispersal mode	-0.04	0	0.03	-0.1	-0.06	-0.04	-0.02	0.02	634	1
b_DispSimpl2Swimmers	Dispersal mode	-0.08	0	0.05	-0.17	-0.11	-0.08	-0.04	0.02	557	1
b_DispSimpl2Walkers	Dispersal mode	0.01	0	0.03	-0.05	-0.01	0.01	0.03	0.07	540	1
b_scaleAx1_nbenv	Sampling properties	0	0	0.01	-0.01	0	0.01	0.01	0.02	530	1.01
b_scaleAx2_TOsptr	Sampling properties	0.02	0	0.01	0	0.01	0.02	0.02	0.03	507	1.01
b_scaleAx3_nbsites	Sampling properties	0	0	0.01	-0.01	0	0	0.01	0.02	575	1
b_Hemeroby_3Mixed:scaleExtent_km2_log	Disturbance * Scale	-0.03	0	0.02	-0.07	-0.05	-0.03	-0.02	0.01	572	1
b_Hemeroby_3Natural:scaleExtent_km2_log	Disturbance * Scale	-0.02	0	0.02	-0.06	-0.03	-0.02	0	0.02	571	1
b_Hemeroby_3Mixed:DispSimpl2Sessile	Disturbance * Dispersal	0.06	0	0.05	-0.03	0.03	0.06	0.09	0.16	580	1.01
b_Hemeroby_3Natural:DispSimpl2Sessile	Disturbance * Dispersal	0	0	0.05	-0.09	-0.02	0	0.03	0.1	720	1
b_Hemeroby_3Mixed:DispSimpl2Swimmers	Disturbance * Dispersal	0.07	0	0.06	-0.05	0.03	0.07	0.1	0.18	581	1
b_Hemeroby_3Natural:DispSimpl2Swimmers	Disturbance * Dispersal	0.06	0	0.06	-0.07	0.01	0.06	0.1	0.18	616	1
b_Hemeroby_3Mixed:DispSimpl2Walkers	Disturbance * Dispersal	-0.03	0	0.05	-0.11	-0.06	-0.03	0.01	0.06	542	1

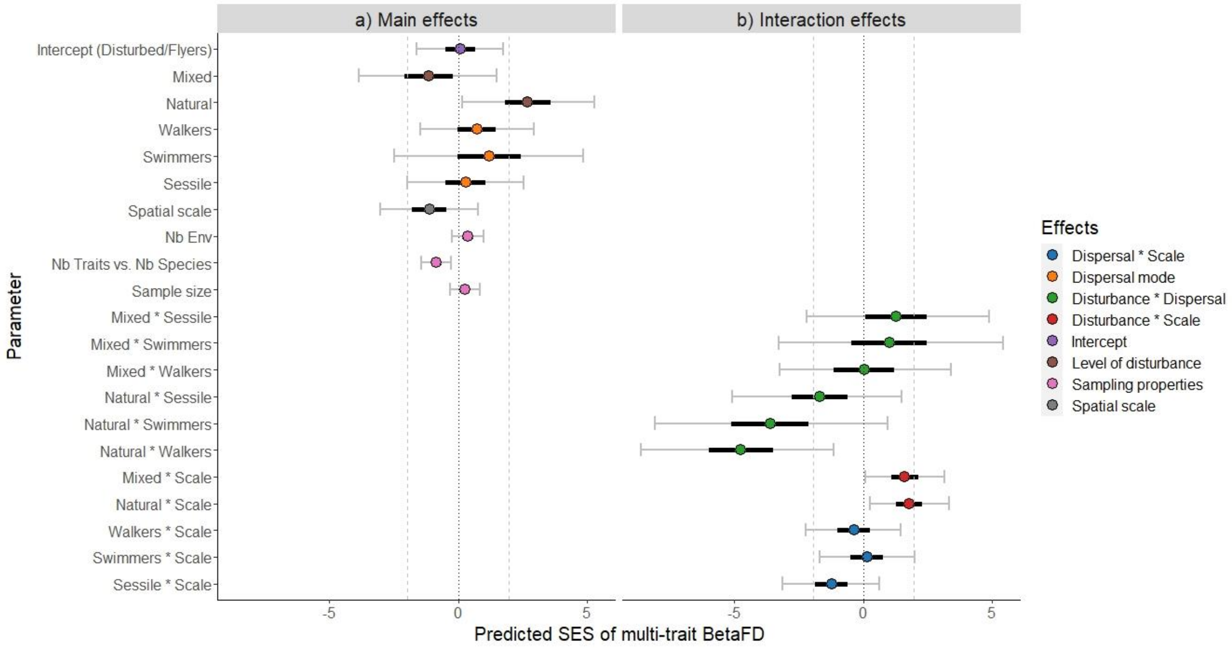
b_Hemeroby_3Natural:DispSimpl2Walkers	Disturbance * Dispersal	-0.1	0	0.05	-0.2	-0.13	-0.1	-0.06	0	634	1
b_scaleExtent_km2_log:DispSimpl2Sessile	Dispersal * Scale	-0.02	0	0.03	-0.07	-0.04	-0.02	0	0.03	568	1
b_scaleExtent_km2_log:DispSimpl2Swimmers	Dispersal * Scale	-0.01	0	0.03	-0.06	-0.02	-0.01	0.01	0.04	577	1
b_scaleExtent_km2_log:DispSimpl2Walkers	Dispersal * Scale	0.01	0	0.03	-0.04	-0.01	0.01	0.02	0.06	642	1
sd_Study3__Intercept	sd_Study3__Intercept	0.04	0	0.01	0.02	0.03	0.04	0.05	0.06	484	1
sigma	sigma	0.03	0	0.01	0.02	0.03	0.03	0.04	0.05	363	1.01
r_Study3[1,Intercept]	Random effect	0.02	0	0.03	-0.04	0	0.02	0.04	0.07	549	1
r_Study3[2,Intercept]	Random effect	0.01	0	0.03	-0.06	-0.01	0.01	0.03	0.07	543	1
r_Study3[3,Intercept]	Random effect	-0.02	0	0.03	-0.1	-0.04	-0.02	0	0.04	563	1
r_Study3[4,Intercept]	Random effect	-0.01	0	0.03	-0.07	-0.03	-0.01	0.01	0.05	596	1.01
r_Study3[5,Intercept]	Random effect	0.01	0	0.03	-0.04	-0.01	0.01	0.03	0.06	600	1
r_Study3[6,Intercept]	Random effect	-0.04	0	0.03	-0.1	-0.06	-0.04	-0.01	0.03	573	1
r_Study3[7,Intercept]	Random effect	-0.02	0	0.04	-0.1	-0.05	-0.02	0	0.04	595	1
r_Study3[8,Intercept]	Random effect	-0.01	0	0.03	-0.07	-0.03	-0.01	0.01	0.05	607	1
r_Study3[9,Intercept]	Random effect	-0.01	0	0.03	-0.07	-0.03	-0.01	0.01	0.05	583	1
r_Study3[10,Intercept]	Random effect	0	0	0.03	-0.05	-0.02	0	0.02	0.05	546	1
r_Study3[11,Intercept]	Random effect	-0.03	0	0.03	-0.09	-0.04	-0.02	0	0.04	616	1
r_Study3[12,Intercept]	Random effect	0.03	0	0.03	-0.02	0.01	0.03	0.06	0.1	484	1
r_Study3[13,Intercept]	Random effect	0.01	0	0.03	-0.05	-0.01	0.01	0.03	0.07	526	1
r_Study3[14,Intercept]	Random effect	0	0	0.03	-0.05	-0.02	0	0.02	0.07	516	1
r_Study3[15,Intercept]	Random effect	-0.01	0	0.03	-0.07	-0.03	-0.01	0.01	0.05	606	1
r_Study3[16,Intercept]	Random effect	0.01	0	0.03	-0.05	-0.01	0.01	0.03	0.08	547	1
r_Study3[17,Intercept]	Random effect	-0.03	0	0.04	-0.1	-0.05	-0.03	0	0.04	585	1
r_Study3[18,Intercept]	Random effect	-0.04	0	0.03	-0.1	-0.06	-0.04	-0.02	0.02	562	1
r_Study3[19,Intercept]	Random effect	-0.05	0	0.04	-0.13	-0.07	-0.05	-0.02	0.02	523	1
r_Study3[20,Intercept]	Random effect	0	0	0.03	-0.05	-0.02	0	0.02	0.06	593	1

r_Study3[21,Intercept]	Random effect	0.01	0	0.03	-0.06	-0.02	0.01	0.02	0.07	596	1
r_Study3[22,Intercept]	Random effect	0.02	0	0.03	-0.05	0	0.02	0.04	0.08	655	1.01
r_Study3[23,Intercept]	Random effect	0.05	0	0.04	-0.01	0.03	0.05	0.08	0.13	584	1
r_Study3[24,Intercept]	Random effect	0.01	0	0.03	-0.05	-0.01	0.01	0.03	0.07	559	1
r_Study3[25,Intercept]	Random effect	0.05	0	0.03	-0.01	0.02	0.05	0.07	0.12	524	1
r_Study3[26,Intercept]	Random effect	-0.07	0	0.03	-0.13	-0.09	-0.07	-0.04	0	498	1
r_Study3[27,Intercept]	Random effect	0.03	0	0.03	-0.03	0.01	0.02	0.05	0.08	567	1
r_Study3[28,Intercept]	Random effect	0.01	0	0.03	-0.05	0	0.01	0.04	0.07	593	1
r_Study3[29,Intercept]	Random effect	0.03	0	0.04	-0.04	0	0.03	0.05	0.1	527	1
r_Study3[30,Intercept]	Random effect	-0.01	0	0.03	-0.07	-0.03	-0.01	0.01	0.05	561	1
r_Study3[31,Intercept]	Random effect	-0.04	0	0.04	-0.12	-0.06	-0.04	-0.01	0.03	499	1
r_Study3[32,Intercept]	Random effect	0.02	0	0.04	-0.05	0	0.02	0.05	0.1	653	1
r_Study3[33,Intercept]	Random effect	-0.06	0	0.03	-0.12	-0.08	-0.06	-0.03	0.01	420	1.01
r_Study3[34,Intercept]	Random effect	0.02	0	0.03	-0.04	0	0.02	0.04	0.08	591	1
r_Study3[35,Intercept]	Random effect	-0.01	0	0.03	-0.06	-0.03	-0.01	0.01	0.05	475	1
r_Study3[36,Intercept]	Random effect	-0.04	0	0.04	-0.12	-0.07	-0.04	-0.02	0.01	526	1.01
r_Study3[37,Intercept]	Random effect	0.03	0	0.03	-0.02	0.01	0.03	0.05	0.09	560	1
r_Study3[38,Intercept]	Random effect	0.02	0	0.03	-0.04	0	0.02	0.04	0.08	557	1.01
r_Study3[39,Intercept]	Random effect	0.01	0	0.03	-0.04	0	0.01	0.03	0.07	352	1
r_Study3[40,Intercept]	Random effect	0	0	0.03	-0.05	-0.02	0	0.02	0.05	613	1.01
r_Study3[41,Intercept]	Random effect	-0.03	0	0.03	-0.09	-0.05	-0.03	-0.01	0.04	628	1
r_Study3[42,Intercept]	Random effect	0.04	0	0.03	-0.02	0.02	0.04	0.06	0.1	557	1
r_Study3[43,Intercept]	Random effect	0.01	0	0.03	-0.04	-0.01	0.01	0.03	0.07	508	1.01
r_Study3[44,Intercept]	Random effect	0	0	0.03	-0.05	-0.02	0	0.02	0.06	623	1
r_Study3[45,Intercept]	Random effect	-0.02	0	0.02	-0.07	-0.04	-0.02	-0.01	0.02	650	1
r_Study3[46,Intercept]	Random effect	0.04	0	0.03	-0.02	0.02	0.04	0.06	0.1	491	1
r_Study3[47,Intercept]	Random effect	0.02	0	0.03	-0.04	0	0.02	0.04	0.08	542	1
r_Study3[48,Intercept]	Random effect	-0.02	0	0.03	-0.08	-0.04	-0.02	0	0.04	455	1

r_Study3[49,Intercept]	Random effect	0	0	0.03	-0.06	-0.02	0	0.02	0.06	663	1
r_Study3[50,Intercept]	Random effect	-0.04	0	0.03	-0.1	-0.06	-0.04	-0.01	0.02	488	1
r_Study3[51,Intercept]	Random effect	0.02	0	0.03	-0.04	0	0.02	0.04	0.09	572	1
r_Study3[52,Intercept]	Random effect	-0.03	0	0.03	-0.09	-0.06	-0.03	-0.02	0.02	566	1
r_Study3[53,Intercept]	Random effect	-0.03	0	0.03	-0.09	-0.05	-0.02	0	0.03	571	1
r_Study3[54,Intercept]	Random effect	0.01	0	0.03	-0.04	-0.01	0.01	0.03	0.07	531	1
r_Study3[55,Intercept]	Random effect	0.02	0	0.03	-0.04	0	0.02	0.04	0.08	591	1
r_Study3[56,Intercept]	Random effect	-0.01	0	0.03	-0.08	-0.03	-0.01	0.01	0.05	668	1
r_Study3[57,Intercept]	Random effect	0.04	0	0.03	-0.01	0.02	0.04	0.06	0.11	623	1
r_Study3[58,Intercept]	Random effect	0.01	0	0.03	-0.04	-0.01	0.01	0.03	0.07	585	1
r_Study3[59,Intercept]	Random effect	-0.01	0	0.03	-0.07	-0.03	-0.01	0.01	0.04	553	1
r_Study3[60,Intercept]	Random effect	-0.01	0	0.03	-0.06	-0.03	-0.01	0.01	0.05	494	1
r_Study3[61,Intercept]	Random effect	0.01	0	0.03	-0.04	-0.01	0.01	0.03	0.06	565	1
r_Study3[62,Intercept]	Random effect	0.01	0	0.03	-0.05	-0.01	0.01	0.03	0.07	519	1
r_Study3[63,Intercept]	Random effect	0.02	0	0.03	-0.04	0	0.02	0.04	0.09	558	1
r_Study3[64,Intercept]	Random effect	0.02	0	0.03	-0.03	0	0.02	0.04	0.08	484	1
r_Study3[65,Intercept]	Random effect	0	0	0.03	-0.06	-0.02	0	0.01	0.06	476	1
r_Study3[66,Intercept]	Random effect	-0.01	0	0.03	-0.07	-0.03	-0.01	0.01	0.05	468	1
r_Study3[67,Intercept]	Random effect	-0.01	0	0.03	-0.09	-0.03	-0.01	0.01	0.04	593	1
lp__	lp	51.17	0.84	16.26	17.83	41.03	52.11	62.63	79.64	377	1.02

Appendix S13. Synthesis plots of multi-trait and mono-trait beta SES

A)



B)

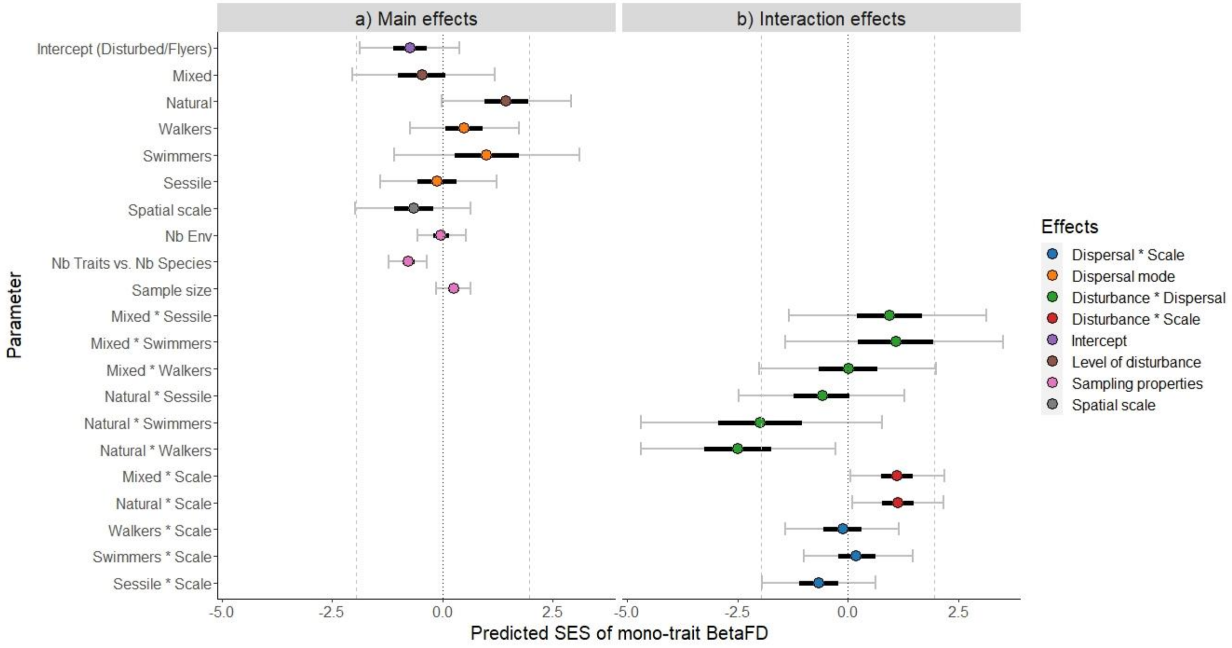


Figure S13.1. Results from the meta-analysis model examining the relationship between the Standardized Effect Size of the A) multi-trait and B) mono-trait Functional Beta Diversity (BetaFD), and a) different ecological features of the datasets: level of disturbance, dispersal mode, spatial extent, and sampling properties (number of sites, number of environmental predictors, and traits-species trade-off), and b) their interactions. Dots are the posterior medians, the black thick whiskers are the 50% confidence intervals and the thin grey whiskers are the 95% confidence interval (results based on BRMS model including a nested random effect on Study|Dataset). Parameters of the model are given in the main MS. The dashed lines represent the thresholds of -1.96 and 1.96 that are used to assess the SES significance as indicator of trait convergence and trait divergence, respectively.